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Trends in Plant Science

Opinion

Phenomics: conceptualization and importance for plant physiology

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Phenomics is a relatively new discipline of biology that has been widely applied in several fields, mainly in crop sciences. We reviewed the concepts used in this discipline (particularly for plants) and found a lack of consensus on what defines a phenomic study. Furthermore, phenomics has been primarily developed around its technical aspects (operationalization), while the conceptual framework of the actual research lags behind. Each research group has given its own interpretation of this 'omic' and thus unwittingly created a 'conceptual controversy'. Addressing this issue is of particular importance, as the experimental designs and concepts of phenomics are so diverse that it is difficult to compare studies. In this opinion article, we evaluate the conceptual framework of phenomics

Highlights

Phenomics has gained popularity in the past 10 years among crop scientists and plant breeders.

Created as an analogue of genomics, phenomics advocates phenotypic-driven analyses to answer complex questions about organisms.

After 20 years since its creation, there is no consensus on a definition of phenomics. As a result, there is a remarkable diversity of so-called phenomic studies.

Plant phenomics has focused primarily on the development of high-throughput tools rather than the theoretical framework.

While the implications of plant phenomics for agriculture are clear, phenomics could help solve complex questions about plant physiology but this requires a clear framework to be developed, as it has been achieved for genomics.

The omics revolution

Over the past two decades, the 'omics revolution' has resulted in the evolution of the discipline of **phenomics** (see Glossary). This new discipline, however, has been practiced and conceived without a conceptual consensus on what it actually entails (see Table 1). Interestingly, the lack of a consensual definition has not hindered the development of phenomics. In fact, it appears that the scientific community is more interested in its technical development and application (operationalization) than the development of its underlying theoretical framework (conceptualization) [1,2]. A scientific discipline, nevertheless, cannot rely solely on technical aspects, as a deep understanding of its theoretical framework is a prerequisite [3]. This has been made evident by the increasing difficulty of establishing correlations between different experimental designs in phenomics as a result of the terminology and definitions varying among studies, as shown in Table 1. As more studies on phenomics are published every year, it has become necessary to bring forward the debate of concrete definitions. This is of fundamental importance, since any scientific discipline needs to define empirical observations (experimental results) in a real-world context, and this is not possible without robust concepts [1,2].

In this opinion article, we analyze the available theoretical framework for phenomics in an effort to standardize the nomenclature and definitions of several concepts used within this discipline. To do so, we started by examining the history and etymology of key concepts used in phenomics (see Table 1). Afterwards, these concepts were analyzed and processed in light of their applicability to the available research (operational procedures). Contrary to other critical reviews, we did not explore the technical aspects of the discipline. Although the present work was mainly intended to guide researchers working in plant physiology, we also compare the use of concepts in various disciplines of biology such as genomics, genetics, and proteomics.

History and etymology of phenomics

What phenomics is seems to depend greatly on who defines it. Some authors define it as a technology; others, as a tool, a discipline, or a synonym of something else such as

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physiology. Table 1 presents some examples of definitions given by several authors. One may question how it is possible that, after almost 20 years, we still lack a consensus on a definition. A possible explanation is that the approach we have used to understand 'omics' is diverse and has changed over the years, especially during the earlier days of the omics revolution [4–6]. This is because, during the formative years of the omics revolution, only genomics and proteomics existed [4–6]. As new omics expanded into other objects of study, the omics concept was used in a broader sense. Omics informally refer to a discipline in life sciences that focuses on the study of abstract objects addressed as '-omes' [7,8]. The suffix '-ome', in the field of molecular biology, is used as a way to refer to the whole or totality of a particular type of biomolecular information [8]. However, -ome is a neologism based on Greek etymology that, according to the *Oxford English Dictionary*, is void of etymological meaning. The -ome must have originated from the combination of the omicron (o) in the Greek etymon of *gene*, γένος (race, offspring), plus -μα(τ), a Greek suffix that informs abstract nouns referring to the outcome of a process, from which we made 'genome'. Nevertheless, there is no '-ωμα' Greek suffix. Therefore, this -ome is a modern suffix.

The name of a particular omic is defined by the prefix of the object of study combined with the suffix -omic. For example, from genome (proposed in 1926 by Winkler) [8], we have genomics (coined by Roderick in 1986) [8]; from proteome, proteomics (both coined by Wilkins in 1995) [8], and so on. Interestingly, even before Roderick coined the term for genomics, the adjective 'phenomic' was used as early as 1949 by Davis. The unspoken rule has its origins in McKusick and Ruddle, who, in 1987, defined genomics as a discipline [9], as well as in Wilkins, when he coined the second omic: proteomics. Surprisingly, genomics (as the first omic) was not originally planned as the name of a new discipline, but only as the title of a scientific journal [8].

The resulting etymological definition of phenomics is a discipline that studies the **phenome**. In turn, a phenome (originally coined by Davis in 1949) could be defined as all the **phenotypes** (via German from the Greek verb φαίνω, 'to bring to light or to cause to appear', plus τύπος in the sense of 'shape' or 'pattern') that a **genotype** or genome could express as a result of the interaction between the external factors (environment) and its developmental plan (see Table 1) [7]. A phenotype must be understood as the set of measurable traits (phenotypic traits) that a particular genotype expresses at a given moment in time. We say 'at a given moment in time' because the phenotype changes according to the developmental stage of an organism as a function of an array of **environmental conditions** (Figure 1). The phenotypic traits could be physical (e.g., color, volume, or shape) [10,11], chemical (e.g., metabolites, enzymes, or internal pH) [10,11], or biological (e.g., development, physiology, or behavior) [10,11]. From our review, an etymological definition of phenomics has seldom been used, but we believe that phenomics should be thought of as a discipline to be considered an omic.

Nevertheless, some definitions (Table 1, e.g., Definitions 9 and 14) explicitly seem to acknowledge the study of large and complex datasets, which is common in an omic. A large dataset, though, is, by itself, a vague concept relative to the analytical capabilities of a research group. Several reports consider that omics require the measurement of the totality of elements of an -ome in a biological model [4,6,8,9,12–15]. Measuring a full phenome is impossible, however, as there is a virtually infinite number of phenotypes integrating the total phenome of a single genotype. For this reason, the completeness of a phenomic measurement cannot be considered a fundamental property of phenomics. Interestingly, most of the studies cited in Table 1 present phenomics as the equivalent of genomics for phenotypes, yet most of these works did not include a definition of phenome.

Glossary

Environmental condition: a set of discrete values consisting of different biotic and abiotic variables, for example, 25°C, soil pH 7, atmospheric pressure 1, altitude 200 m above sea level, under 45% humidity, an irradiance of 300 μmol of photons m^{-2} s^{-1}.
Environmental variables: a continuous environmental factor, e.g., temperature (20.9°C, 24.3°C, 32.1°C, etc.) or pH (4, 7, 10, etc.).
Epigenetic factor: a factor that affects the expression of the genetic code without altering its sequence. This factor could appear as a response to the environment or be part of the developmental plan of an organism.
Genotype: the set of genes of an individual organism or group of organisms regarding a single trait, a subset of traits, or the entire set of traits.
High-throughput phenotyping: a method through which the output process of phenotyping is increased through automation, imaging, or a combination of both. High-throughput phenotyping is necessary for phenomics, but not every screen carried out by high-throughput phenotyping is phenomics.
Manageable phenome: the portion of the phenome where reasonably measurable phenotypic characteristics and responses reside. In other words, an organism's response to the relevant environmental variables of interest to the investigator. One does not need to measure the plant's response to all environmental conditions and at all time intervals that show a change in traits, but only those that are meaningful.
Phenome: a hypervolume formed by all the phenotypes that a genotype can express as a result of the interaction between its genetic code and the epigenetic factors.
Phenomic study: a study through which the phenome and its structure of a genotype are examined.
Phenomics: biological discipline that focuses on the study of the phenome.
Phenotype: the set of observable traits, which could be either physical, chemical, or biological, expressed by a genotype at a given time.
Phenotyping: to allocate a phenotype.
Screening: in the context of phenomics, the examination or analysis of organisms to check for the presence of desirable or undesirable elements or attributes, or to assess the suitability for a particular purpose by using phenotypic traits.

Table 1. Examples of definitions of phenomics and the phenome, in chronological order

No.	Author	Year	F[a]	Definition of phenomics	Definition of phenome	Type[b]
1	Davis [20]	1949	Gn	Not included	'The sum total of extragenic, nonautoreproductive portions of the cell, whether cytoplasmic or nuclear'	
2	Soulé [50]	1967		Not included	'The phenotype as a whole'	
3	Schork [16]	1997	M	'A discipline … which attempts to unravel biochemical and physiological hierarchies leading from genes to clinical endpoints' 'The delineation of connections among various genes, gene products, intermediate phenotypes, and clinical endpoints'	Not included	Tech
4	Dove [51]	1999	B	'An all-embracing term (on a par with genomics) to describe functional genomics'	'The full set of phenotypes of an organism'	Disc
5	Schilling *et al.* [18]	1999	Gm	'The study of the genotype–phenotype relationship, through the use of genomic data and analysis of multigenic functions'	Not included	Tequ
6	Paigen and Eppig [14]	2000	M	Not included	'[The inference of] the average, or sum, of phenotypic traits measured within and across strains, recognizing the importance and experimental value of phenotypic variation'	
7	Motulsky [13]	2000	Gm	'The broad study of the phenotype that must be carried out in conjunction with genomics'	Not included	Disc
8	Evans [4]	2000	Gm	'To quantify the functional expression of genetic variation'	Not included	Res
9	Evans [5]	2000	Bt	'The complete set of mutational phenotypes'	Not included	Obj
10	Palsson [52]	2000	Bt	'A study of phenotypes with knowledge of the genotypes'	Not included	Disc
11	Gerlai [53]	2002	N	'The behavioral and other phenotypic analyses designed to obtain a large amount of information on the varying effects of genetic mutations'	'The phenotype as a whole'	Tequ
12	Bogue and Grubb [15]	2004	M	Not included	'The physical totality of all traits of an organism'	
13	Freimer and Sabatti [12]	2003	Gm	'The investigation of the phenome … Phenotypes, like genotypes, can, by definition, vary between individuals, and it is this variability that phenomics seeks to understand'	'The expression of the genome as traits in a given environment'	Disc
14	Sauer [37]	2004	B	'Large-scale experiments for generating gene disruptions and analyzing phenotypes … to ascertain gene function. Any form of phenotypic analysis of genomic information or entire mutant collections with the goal of understanding the relationship between genes and higher levels of organization in the cell.'	Not included	Tequ
15	Houle [11]	2010	Gm	'The acquisition of high-dimensional phenotypic data on an organism-wide scale'	Not included	Res
16	Furbank and Tester [35]	2011	P	'Plant phenomics is the study of plant growth, performance, and composition'	Not included	Res
17	White *et al.* [33]	2012	P	'Research to improve phenotyping techniques'	Not included	Res
18	Rahaman *et al*. [7]	2015	P	'An emerging and increasingly important branch of biological sciences termed 'phenomics' … Phenomics is a technology that enables high-throughput phenotyping for crop improvement'	Not included	Tech
19	Tardieu *et al*. [32]	2017	P	'The development and application of the suite of tools and methods used for three major goals: capturing information on structure, the function and performance of large numbers of plants, together with their environment; analyzing, organizing, and storing the resulting datasets; and developing models able to disentangle and simulate plants' behavior in a range of scenarios'	'The complete phenotypic representation of the species'	Res

[a]The Field (F) column indicates the main discipline of the article: P, plant sciences; N, neurosciences; Gm, genomics; B, biotechnology; Gn, genetics; M, medicine.
[b]Type refers to the area on which the differentia of the definition of phenomic are focused: Tech, technology; Disc, discipline; Res, research; Obj, object; Tequ, technique.

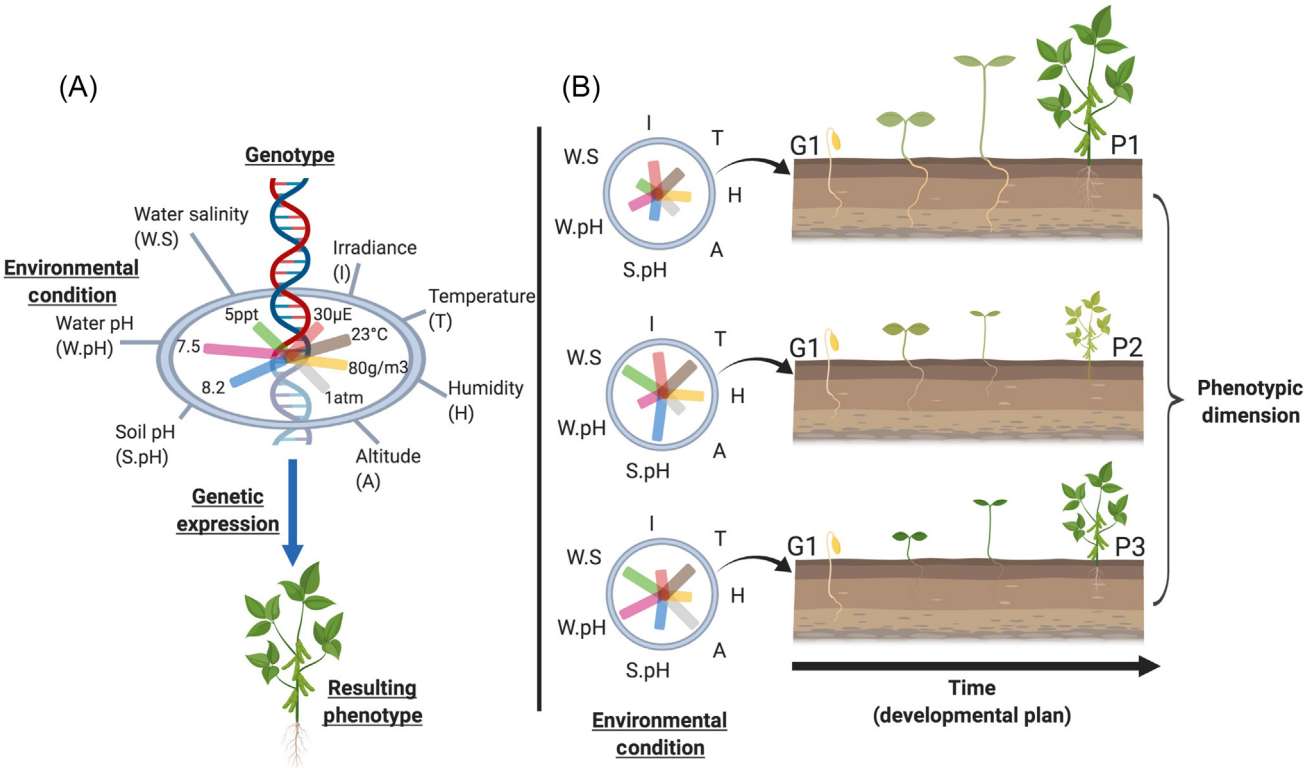

Figure 1. Conceptualization of the interactions among the genotype, the environment, and the resulting phenotype. The phenotype is the set of phenotypic traits that a genotype (an organism with a certain genetic sequence) expresses at a given time due to its developmental plan in relation to the environment. The left side (A) of the figure shows a conceptualization of a genotype's interaction with a set of environmental conditions. The right side (B) shows the same interaction across three separate environmental conditions and the resulting phenotype. In this example, a seedling could grow at different rates and express different phenotypic traits depending on the environmental conditions that it is subject to. The results of a single genotype exposed to three different environmental conditions show a variation in growth rate and color. Figure created with biorender.com. Abbreviations: A, altitude; H, humidity; I, irradiance; S.pH, soil pH; T, temperature; W.pH, water pH; W.S, water salinity.

We have not been able to determine an exact start for works on phenomics, but we have identified the work of Schork in 1997 [16] as the first to provide a proper definition:

> '…a new discipline, "phenomics" or "phenometrics," could be initiated that would complement genomic research as presently performed … [Phenomics] attempts to unravel biochemical and physiological hierarchies leading from genes to clinical endpoints.'

Schork's report was published only 2 years after the term proteomics (the second great omic) was coined and, by 2000, several works were advocating for its use and development. Interestingly, many of those early works that used the term never defined it. Moreover, the term appears to have been coined independently by many authors who were not aware of each other's work [6,13,14,16–19].

What makes a phenome?

In 1949, Davis [20] proposed the concept of a phenome as 'the sum total of extragenic, non-autoreproductive portions of the cell, whether cytoplasmic or nuclear. The phenome would be the material basis of the phenotype.' Nowadays, we refer to these 'extragenic' factors as '**epigenetic factors**' [21] and understand that they induce a particular phenotype [22] by regulating genetic expression. Nevertheless, one should not forget that a phenotype is also caused by the developmental

plan [23–25]. It is important to point out that, in this text, we make a distinction between **environmental variables** and environmental conditions (Figure 1). A phenome is a function of the environmental variables, while phenotypes are a function of a set of environmental conditions.

Some definitions of a phenome focus only on those phenotypes that originate from the effect of environmental factors rather than genetic expression (Table 1). If we accept this as a valid criterion, then all studies that deal with phenotypes caused by the developmental plan are not part of the phenome. As a consequence, studies focusing on these phenotypes could not be considered phenomics. Because there are several **phenomic studies** published on the developmental plan (such as leaf senescence monitored across the lifecycle via phenomics [26–29]), using a definition in which the environment is the only component acknowledged is somewhat impractical.

Synthesis for the definition of phenomics

In light of the etymology and the characteristics of the phenome, it would be suitable to introduce a formal definition for phenomics. If phenomics is to be thought of as an omic, it must have an -ome as its object of study, which is, in this case, the phenome. Therefore, a simple yet accurate definition of phenomics is 'the biological discipline that studies the phenome'. This definition contains the basic requirements, namely a category (the genus, a subdiscipline of biology, etc.) and an object of study (differentia) which make this omic different from any other element within the same category (biological omics). The main advantages of this definition, based on classical logic, are that it offers a concrete object of study, it is logical, and it covers most of the works self-identified as phenomics.

Therefore, a more relevant question is what the phenome is. It can be defined as the set of expressed phenotypes of a given genotype or genome (G) in relation to epigenetic factors, which are dependent on the time (t) and the environment (E), thus $t \times E$. Consequentially, phenomics entails the sets of phenotypes and the structure of such a set in relation to the factors that caused their expression ($G \times t \times E$).

What makes phenomics different from other biological sciences?

Because some studies of ecophysiology or epigenetics that have considered the matrix $G \times t \times E$, it is enticing to think that phenomics is just a synonym for something that already existed. However, ecophysiology and epigenetics have different objects of study *per se*. For example, ecophysiology's object of study is the relationship between the ecosystem and physiology, not a given phenome and its structure. For this reason, we propose that what makes a phenomic study different is the focus on the phenome and its structure.

To better understand how phenomics operates, we need to describe some core attributes of the concept of a phenome. First, the phenome is a set of phenotypes originating from $G \times t \times E$. The elements of a phenome, the phenotypes, are products of these dimensions and are localized in this multidimensional space. Because the environment is multidimensional (each environmental condition is a dimension, e.g., pH, temperature, or humidity), the phenome is a hypervolume, as it has more than four dimensions. The relevance of dimensionality was first acknowledged by Houle [11], and we consider this as characteristic of any phenomic dataset (Box 1). Therefore, it is expected that phenomic studies be multidimensional, although multidimensionality is not what defines phenomics.

Another attribute of phenomic studies considered to be a key feature has been large datasets (as seen in Table 1). A large dataset is, however, an ambiguous abstraction. Of course, as the phenome is virtually infinite, any dataset focusing on a phenome will inherently be large. Caution is advised, nevertheless, when defining whether a dataset is or is not phenomic. In some cases,

Box 1. A case study demonstrating the data structure of the phenome

Genotypes are represented as DNA strings that are exposed to environmental conditions, and the phenotype is measured over time. The resulting equation at the bottom of each panel represents the complexity of the study: genotypes are represented as *g*, phenotypic traits as *Trait*, and time as *t*. Experiment 1 (Figure IA). Let us consider a comparative study of a mutant versus a wild-type grown under the same conditions and phenotyped by light-induced fluorescence transients (LIFT) chlorophyll fluorometry. This example would never be considered to be a phenomic study but a classic photophysiology study. Let us extend this study by including time as a variable, in which the samples are measured 12 times a day for over a year. The amount of data obtained would be large (4380 measurements with a large number of derivate parameters) for each of the two genotypes, yet this study does not involve phenomics. Nevertheless, the study would have required phenotyping and would have yielded a large dataset. Experiment 2 (Figure IB). By contrast, a simple phenomic study would be one of the four genotypes exposed to four environmental conditions, measuring four phenotypic traits. For example, one wild-type *Arabidopsis thaliana* and three mutants were grown at four temperatures (15°C, 20°C, 25°C, and 28°C), for which pulse amplitude modulated (PAM) chlorophyll fluorescence, leaf area index, leaf reflectance, and height were measured. This type of study would be a phenomic study, despite the fact it only explores four environmental conditions. One could further expand its dimensionality by measuring these variables three times a day from germination to senescence. In such a case, the complexity would have been extended and the required phenotyping would be intensive. Experiment 3 (Figure IC). Finally, let us imagine a study with four genotypes grown at eight light levels and four temperatures in which the same phenotypic traits were measured across their lifecycle, as in the second example. This study would undoubtedly be considered a phenomic study because not only would a large dataset be generated, but the phenome would also be better resolved.

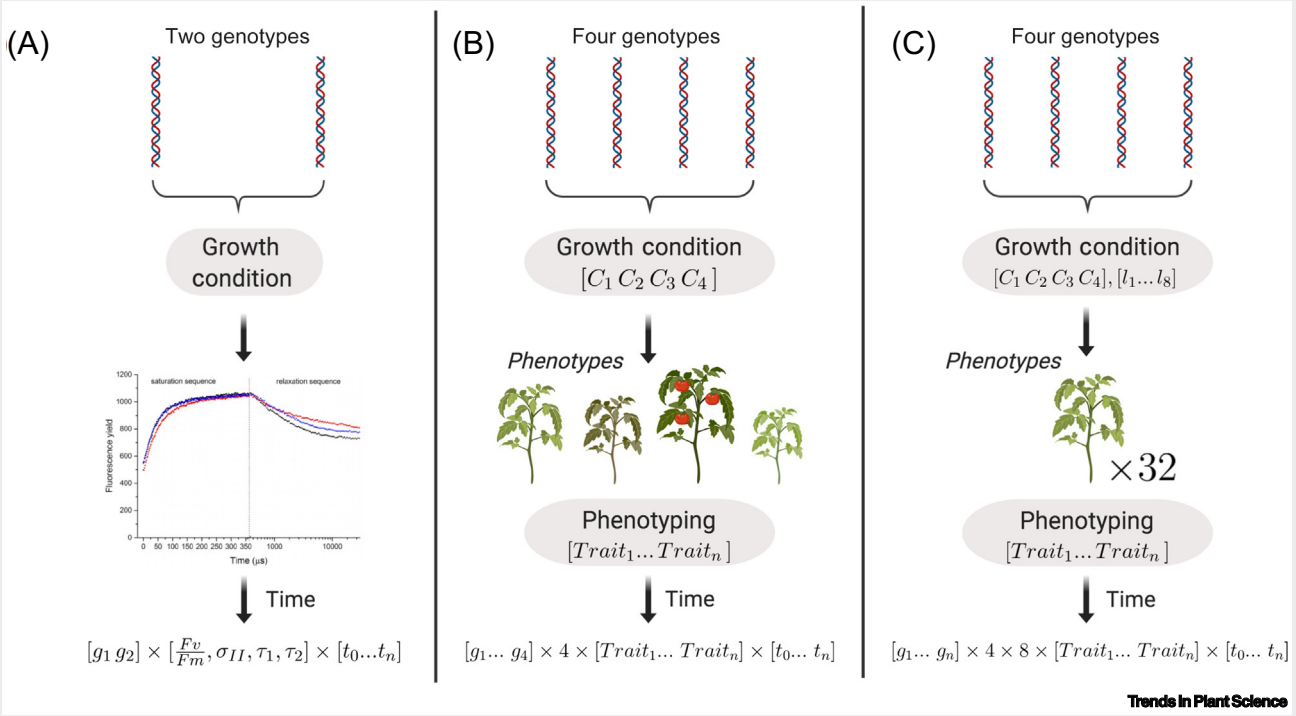

Figure I. Three examples of experiments to demonstrate how multidimensionality in an experimental design defines a phenomic experimental structure. (A) Experiment 1. (B) Experiment 2. (C) Experiment 3. Figure created with Biorender.com. Abbreviations: *C*, growth condition; F_v/F_m, photosystem II activity; *τ*, lifetime; *t*, a given time point.

large datasets may originate from tens of genotypes studied under the same condition; in others, they could originate from hundreds of genotypes exposed to several environmental conditions. Therefore, is there a simple notion of a phenomic dataset? Since phenomic data originate from a set of phenotypes resulting from the relation G × t × E, an ideal phenomic dataset should include all these components. It should also be noted that the component of time, regardless of being explicitly acknowledged in a phenomic study, is always part of any experimental design.

Do we need high-throughput phenotyping to carry out phenomics?

Scientists obtain phenomic knowledge by allocating a phenotype (**phenotyping**), but large-scale phenotyping is not enough to obtain phenomic data. Phenotyping was coined as a verb as early

as 1952 (by Allan at *The Lancet* 1952 [30]) and is not a concept exclusive to phenomics, for it has been used in other biological disciplines as well, such as genetics and plant physiology. The example in Box 1 shows that it is not the size of the datasets or the large-scale phenotyping that makes a phenomic study. In our opinion, what makes a phenomic study is that the datasets comprise a set of phenotypes of well-defined genotypes or genomes in well-defined environmental conditions. Such datasets are, by default, multidimensional: 4D or higher. If a study does not contain the basic dimensions that compose a phenome, it cannot be considered a phenomic study because it is not studying a phenome but other phenomena.

For instance, the first experiment (see Figure IA in Box 1) compares two genotypes (the genomic dimension) and their photosynthetic behavior (the phenotypical dimension) across time (the temporal dimension). But it lacks an environmental dimension (a single point), since only one growth condition is studied. Therefore, the study is only three-dimensional. One might understand this experiment as a 4D structure, for there is an environmental setting within which the phenotypical dimension is resolved. However, as this experiment includes no complementary environmental conditions (i.e., an alternative temperature), the environmental dimension is not considered in the analysis. The second type of experiment compares four genotypes (the genomic dimension) exposed to one varying environmental condition (the thermal dimension) and four phenotypic traits (which are all part of the phenotypic dimension) across time (the temporal dimension). Finally, the third experiment considers four genotypes (the genomic dimension), two environmental dimensions, and four phenotypic traits (the phenotypical dimension). The last two experiments would generate phenomic datasets since they have the basic dimensions and include at least four dimensions.

In Box 2, we present a graphical representation of the organization of phenomic data. As the dimensionality expands in a phenomic study (e.g., as more environmental conditions are included), the complexity increases but so does the resolution of the phenome.

Phenomics is all about manageable phenomes

Because the absolute phenome is virtually infinite, researchers must approximate it by constraining their experimental investigations. Then, by focusing on meaningful phenotypic traits and a subset of environmental conditions that are derived into manageable and meaningful datasets or **manageable phenomes**, one can perform a comprehensive analysis of the phenomic data.

Do we need the genomic data for phenomics?

If phenomics has the study of a hypervolume generated by G $\times$ E $\times$ t as its objective, then it is logical to assume that genotypic information is basic to phenomics. However, a new term, 'functional phenomics' [31], has been proposed to describe a subtype of phenomics that could operate without a 'simultaneous study of the underlying genetics', focusing primarily on plants' functions; in other words, E $\times$ t. We find this paradoxical since, in phenomic studies, the phenome does not exist without the genomic dimension, as illustrated in previous sections (Box 2).

Large-scale phenotyping and the power of a phenomic study

A common association with phenomics is large-scale phenotyping. In fact, some authors have matched the concept of phenomics to **high-throughput phenotyping** [7,32,33]. As we explained in previous sections, however, phenomics is more than just a method, a technique, or a technology. Nevertheless, high-throughput phenotyping is a requirement if one aims to resolve a phenome with great resolution (Box 2). Associated with this aspect of phenomics is the concept of **screening** and the generation of reliable data. A reliable phenomic dataset would result from intensive sampling (in fine detail, i.e., chemical profiles) performed through extensive screening (large coverage over a long time or area) for as long as is technically feasible (a manageable phenome).

Box 2. Concept of increasing dimensionality visualized and discussed

By definition, a phenome is the product of at least four dimensions: genomic, temporal, phenotypic, and at least one environmental dimension. As a phenome is the set of phenotypes (Figure IA), a phenotype is $P_{e,t} = \cup_i^n T_n$, where P (represented by the colored circles) is a phenotype expressed in a given environmental condition (e) at a given time (t); simultaneously, it is the set of all traits (T) from i to n (note that $e, t, n \rightarrow \infty$). Note that, here, we are using the operator '$\cup_i^n$' (the union of element i to element n) to refer to the set of phenomic traits included in any given study. Because it is virtually impossible to measure all the traits in an organism, here we refer to it as a set of traits decided by the researcher (i.e., a manageable phenome). The greater the number of traits measured to describe a phenotype, the higher the resolution of the phenotype. In addition, the greater the number of phenotypes (P) identified per genome in a study, the better the phenome is resolved.

The reader should note that a high-resolution phenotyping system improves the detail of a phenotype, but it does not necessarily make a phenomic study. Moreover, increasing the number of genotypes *per se* does not improve the resolution of a phenomic study, unless one is interested in the phenome of a whole species (sp. phenotype). For this reason, a phenomic dataset is but a hypervolume defined by several dimensions (multidimensionality) (Figure IB). Concomitantly, the greater the number of dimensions (external factors used to generate the phenotypes), the higher the resolution of the phenome. This is illustrated by Figure IB, which shows how the resolution of the phenome increases along with the number of dimensions.

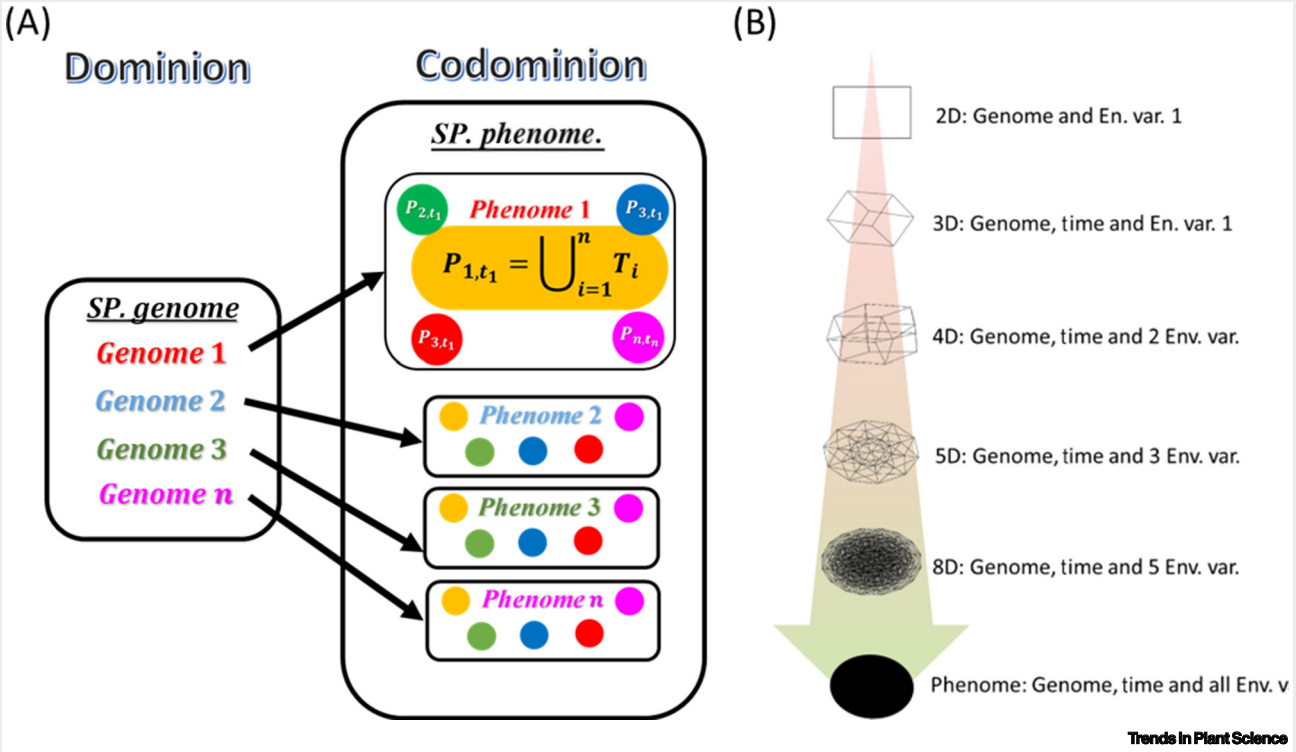

Figure I. Phenomic data structure. (A) Set theory of a phenome. (B) Dimensionality of the phenome. Abbreviations: En. var., enviromental variable; Env. var., enviromental variables; P, a given phenotype; T_i, phenotypic trait.

What are the implications for having a concrete definition of phenomics for plant and algal physiology?

Researchers have recognized the benefits of phenomics for plant breeding [7,10,32–35] since phenomics can be used in conjunction with other omics [4,32,36,37]. It has also been concluded that the ultimate goal of plant phenomics is to close the gap between genomics and agricultural sciences [10,35,38]. It is also possible, however, that phenomics will answer basic questions in plant physiology. This latter interest is where the definition of phenomics proposed here will be more useful, as it expands the understanding of phenomics beyond its applied benefits. Available examples are the variations in the expression of mutations in different environments [39], studies of the complex

interactions of plants and pathogens [40], or even ecophysiological studies on the genotypes of crops [41]. In the near future, phenomics will likewise answer ecophysiological questions (for a detailed commentary, see [42]), because, up to now, answers to such complex questions are frequently obscured due to genetic variability. Another example is the use of phenomics in the study of microalgal physiology. While plants' photochemistry is more stable in response to the environment, the photophysiology of algae is highly variable, depending on the growth cycle, light conditions, temperature, etc. [43,44], all of which induce rapid changes in the photochemistry and, therefore, the phenotype. This makes photophysiology unpredictable due to microalgae's highly plastic phenotype. For example, studies on the mechanisms of photodamage to photosystem II [45–47], the importance of reactive oxygen species during light stress [45,46], the relevance of non-photochemical quenching as a photoprotection mechanism [45,46], or the relevance of state transitions [48,49] have all yielded different results, since each study used different species, grown under different conditions. These discrepancies could be resolved by using phenomics and measuring different strains of microalgae over a range of relevant conditions.

Concluding remarks

On the basis of a critical review of the literature, we advocate for the definition of phenomics as the discipline of biology that studies a hypervolume named the phenome and its structure. The phenome consists of all the possible phenotypes that a given genotype or genome could express as a result of the environment and the developmental plan. Our opinion is based on practical, linguistic, philosophical, and mathematical considerations. We are aware that some of these terms and ideas may not be widely accepted *ipso facto*, but their proposal will create awareness in our field of the need to debate the present terminology and unravel the conceptual controversy (see Outstanding questions).

Outstanding questions

Will phenomics aid in answering unresolved questions relating to unknown mechanisms of plant physiology?

Given that we have access to several phenotyping tools, what key questions can be solved by phenomics approaches?

From what is available in the published corpus of phenomics, can all of it be identified as actually being phenomics?

What is the limit to resolving a phenome?

Is there a way to define the minimum size of a phenome to be studied?

Is it possible to study phenomics without genetic information?

What new types of phenomics will appear? Will phenomics follow the footsteps of genomics in this regard?

Crop sciences and phytopathology will clearly benefit from phenomics, but what about other areas in which plant sciences have great relevance, such as toxicology, ecology, ecophysiology, oceanography, etc.?

Given the parallelisms between plants and algae, can algal phenomics be modelled on plant phenomics?

In case of algal photophysiology, are the contrasting models used to describe their photophysiology correct, and are the differences among each of these models the result of phenotypic plasticity?

Author contributions

All authors contributed to the writing and the design of the figures in this opinion article.

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Declaration of interests

The authors declare no conflict of interest.

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