

Plant systems biology

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Introduction

The concepts of reductionism and holism dates back to the time when true value of science and scientific basis of concepts gained recognition. Reductionism believes in starting from individual components and then moving towards total conduct of the system. On the other hand, holism favours the consolidated nature of systems, to view it as a discrete entity. The concept of holism can be traced back, from the Aristotle's *Metaphysica* which says "The whole is greater than the sum of its parts". Science finds its roots in reductionism right from its infancy. Reductionist thinking still holds a significant influence on science, including biology, especially after the rise of molecular biology which interpreted life being guided by molecular means including heredity. Molecular biology is grounded in reductionist views wherein complexity of biological systems is explicated in terms of the physicochemical properties of the individual components. The reductionist understanding, finds its roots, way back in the exemplary the one-gene one-polypeptide hypothesis of Beadle and Tatum, who actually demonstrated the direct relationship of the genotype to the phenotype at the molecular level.

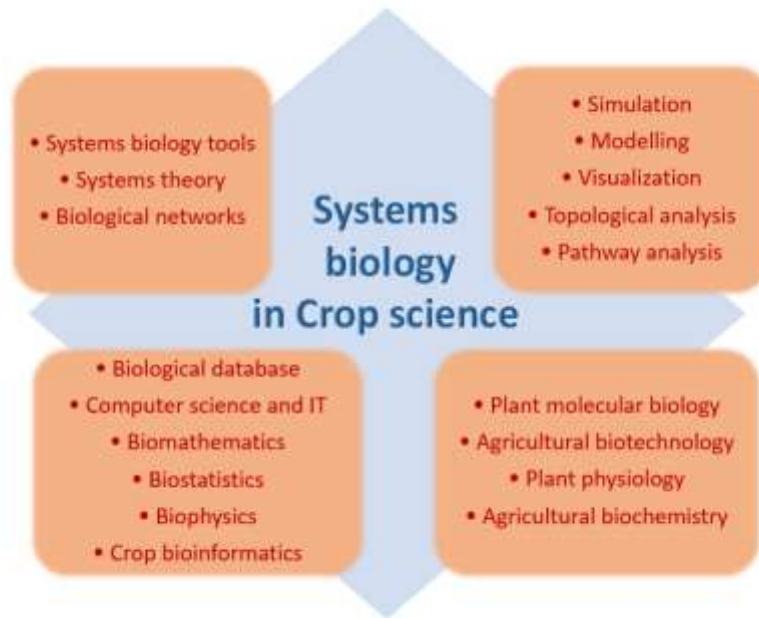
Although as far as the interpretation of the data into meaningful information is concerned, bioinformatics has been crucial in every aspect of omics based research to manage various types of genome-scale datasets efficiently and extract valuable knowledge. However, with the passage of time, the limitations of the reductionist molecular approach have become increasingly evident. It became evident that biological systems cannot be explained only at the genetic level. Instead they should be understood as complex systems resulting from dynamic interactions of different components at different levels, each individually functioning as wholes, which eventually control the phenotype. Complex systems exist at different levels of biological organization ranging from the subatomic realm to individual organisms to whole populations and beyond. Hence a need arose for an integrative framework, which provides a holistic understanding of the biological systems. This new realm of science, in the postreductionist era, is called systems biology.

Systems biology is an approach by which a system of interacting units is analysed as a whole rather than by analysing its individual constituents separately. Systems biology has actually enabled the maturation of science from a data collection enterprise to an explanatory endeavour.

Biological systems and systems biology of plants

The biological communities, differing in their form, structure and habitat extend across the entire biosphere. Complexity and robustness are the key features of biological systems. Robustness plays a key role in maintaining the appropriate functioning of the complex system despite internal/external perturbations (e.g., stochastic noise, physiological and developmental signals, environmental change and genetic variation). A thoughtful examination of the biological systems is indispensable to predict the effects of developmental programs, natural or human-induced perturbations on the composition and function of biological systems. The molecular interrogation and investigation of a complex system, along with maintenance of a global perspective is needed to understand the system function is eventually a key challenge to biological intellect. The various levels of biological systems' organization include cells, molecules, organelles, tissues,

organs, biochemical pathways, and whole plants and so on. The systems biology focuses on integration and not the dissimulation of the parts below the cellular level and hence the biological systems extend toward levels such as genome, transcriptome, proteome, metabolome, interactome and cellome. To gain a comprehensive idea, the assimilation of the networks at different levels of biological organization involving experimental and computational modelling approaches is required.



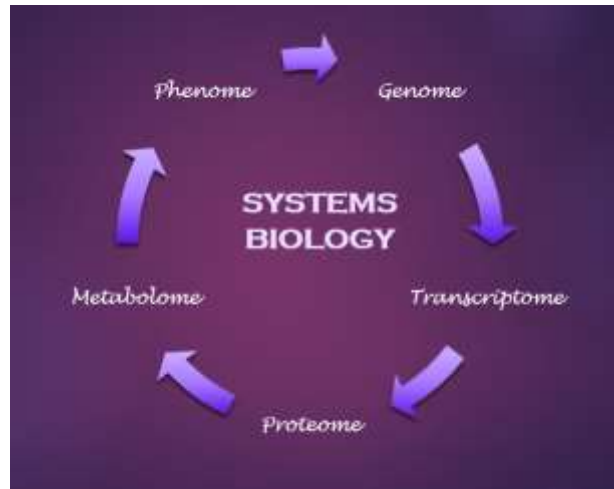
Systems Biology: A consolidation of multiple approaches

Plant systems biology

Plants are greatly suited for systems analyses as they are easy to handle, quite good production of offspring for genetic analyses and many have comparatively short generation times. Hence modelling of plant biological phenomena can be accomplished in a quick, reiterative way by means of using the abundant molecular tools available. The rationale behind increasing interest in systems biology is the prospects and progress in high-throughput genomics and proteomics technologies facilitating the researchers on building ample datasets with relevance to differing plant response. Systems biology aids in our understanding of the plants using holistic systems approaches. Plant systems biology resides at the intersection of physiological, morphological, molecular, biochemical and genetic information applied to plant biology. The need for the subject arose with necessity to integrate and interpret large datasets of high-throughput genomic, transcriptomic, proteomic, metabolomics technologies. Despite the enormous efforts in generation of huge experimental datasets, the work done on the side of development of computational platforms to analyse and decipher the data in form of biological model remains scanty. Thus, plant systems biology encompasses the studies on plants in response to biological, genetic or chemical perturbations which includes supervision of gene, protein and biochemical pathways; application of omics approaches, integration of the data; and formulation of mathematical models that describe the structure and function responsive to the individual

perturbations in form of biologically meaningful perturbations.

Components:



Genomics

Genomics means the study of the organism's whole genome. It lies at the base of the complex plant systems' hierarchy and it provides an understanding toward the organisms' behavioural explanation, and hence is a scientific discipline in its own premise. The earlier molecular perspective to resolve the ambiguities in plant identification and discrimination included various molecular techniques viz. PCR, RFLP, AFLP, RAPD and sequencing. The era of single gene sequencing marked the beginning of plant genomics followed by whole genome sequencing, single nucleotide polymorphism (SNP) and medium density arrays, and eventually led to the current whole genome resequencing. As such, it is a prerequisite for understanding the role of the genes in the development of an organism, hence acting as a driving force from the genomics to the systems biology approach for gaining an insight in the totality.

Genome-wide association studies (GWAS)

The interaction of the individual genes with the environment enables an organism to produce a phenotype. Many phenotypes are quantitative in nature, and complex in etiology, with multiple environmental and genetic causes. There are innumerable examples of quantitative traits in plants viz. plant yield, flowering time, sugar content, disease resistance and fruit weight, which result from the segregation of many genes and are influenced by environmental interactions. The classical approach to study the complex quantitative trait loci (QTLs) was linkage analysis.

Epigenomics

Phenotypic variation is usually attributed to genetic variation corresponding to the nucleotide sequences during the course of evolution. The candidate gene and genome wide analyses are imperative for mapping the genotype-phenotype relationship. Over a long span of time, numerous biological phenomena like paramutation, parental imprinting, control of transposon activity and transgene silencing, failed to be understood by the classical mendelian notion of inheritance of acquired traits, long before their molecular details were known. These phenomena

overruled the Mendelian laws and appeared to follow the non-mendelian mode of inheritance. The intensive efforts to find suitable reasons and mechanisms underlying, these apparent 'exceptions' to Mendelian suppositions have led to shaping a new field of 'epigenetics' (literally meaning 'above genetics'). In current scenario, epigenetics is the study of heritable changes in gene expression and function that cannot be explained by changes in DNA sequence. The epigenome refers to the description of various epigenetic regulators across the whole genome.

Transcriptomics

The term 'transcriptome' encompasses all the genomic counterparts which are expressed as RNA transcripts, including coding (mRNA) and non-coding (e.g., tRNA, miRNA) RNAs at a given time in a cell or population of cells under a given set of environmental conditions. Unlike the traditional transcriptional analyses that comprised of northern blots, the modern methods of transcriptome elucidation include microarray analysis and NGS technologies. Microarray technology has been used since past many years and has matured into developing our insight toward gene regulatory networks and their behaviour under varying environmental conditions.

Proteomics

Proteome, termed by Wilkins et al. (1996) is the entire protein complement of the system, expressed at a given time and under-defined environmental conditions. The systemic analysis of the proteome is called proteomics. The complexity of the proteome is much greater than that of the transcriptome due to the huge amount of possible post-translational modifications, making the former highly dynamic. Proteomics basically deals with analysing changes in protein expression, study of protein structure, function and post-translational modifications that majorly include phosphorylation and ubiquitination.

Metabolomics

The term "metabolome", suggested by Oliver et al. (1998), includes the entire set of small molecule metabolites, produced by any organism. Metabolomics is the comprehensive analysis of all the metabolites under given set of conditions, in an organism. The set of metabolites in an organism, represents more heterogeneity compared to genes and proteins in terms of their physical and chemical properties, varying widely with respect to size, polarity, quantity and stability. Metabolic profiles provide a biochemical phenotypic assessment of the plants and hence are the most valuable in systems biology studies, so regarded as a cornerstone of systems biology.

Interactomics

The functioning of a cell or any system is attributed to the dynamic and harmonized interactions of its macromolecular constituents, like DNA, RNA, lipids, proteins, and other small molecules, with varied biochemical properties. Amongst these, the protein-protein interactions are most abundantly reported followed by the DNA/RNA-protein interactions in plants. DNA-protein interactions include the histone proteins bound to DNA to form the chromatin structure, which function in the epigenetic regulation of various physiological processes, discussed earlier. Thus, interactomics, the comprehensive analysis of the interactions between different macromolecules, predominantly protein-protein interactions in an organism, is critical to our understanding of the cellular systems.

Other ‘omics’ approaches

Apart from the chief omics approaches discussed earlier, some recent approaches include lipidomics (comprehensive study of the lipid entities of the organism) and hormonomics (the entire set of endogenous hormones in a plant). The low molecular weight plant hormones include auxin, ABA, cytokinin, gibberellins, ethylene, brassinosteroids, jasmonates, salicylic acid and a newly identified one—strigolactone (acting as a shoot branching inhibitor); lectinomics (bioinformatics studies of carbohydrate-binding proteins—lectins) and various others. Also, a new concept which has gained much attention in this era is that of phenomics’, the high-throughput systemic analysis of phenotypes, which has probably the biggest application in plant biotechnology.

Integration of multiple ‘omics’ data

The advances in high-throughput analytics have enabled us to gain insights of individual biomolecules with the help of various ‘omics technologies’ discussed in the previous section. However, any single ‘omics’ approach may be inadequate to characterize the complexity and behaviour of biological systems as a ‘whole’. Hence the molecular research is gradually shifting toward the holistic perceptions of systems biology, by integration of the individual ‘omics’ datasets, to gain biologically meaningful interpretation of the plant systems. Therefore, integration of multiple layers of biological information will provide a precise ‘picture’ of the ‘whole’ plant systems. The integration of the multiple omics datasets must be carried out after they are preprocessed (normalization, missing value attribution and feature selection). Data integration is a key to the successful development of the systems philosophy by building comprehensive models of plant systems. Given the enormous promise of integration of the multiple omics data, logical input to the designing of various experiments and analysis of the heterogeneous data is gaining interest. The successful integration of data will depend on appropriate experimental design, sound statistical analysis and correct interpretation of the results.

Softwares and algorithms for plant systems biology

The use of bioinformatics’ softwares is inevitable for the comprehensive study of plant systems biology. In addition to the tools and resources used in the analyses of the individual ‘omics’ platforms, several resources are required for the elucidation of the ‘complete picture’. The detailed discussion of various algorithms and softwares used for systems biology are listed in Joyce and Palsson (2006) and Turenne (2011). These include the tools for network visualization, modelling environments, pathway construction and visualization tools, systems biology platforms and repositories of the models. Visualization is a means of investigative data analysis and a key method for network analysis. The purpose of omics data visualization should be to create clear, meaningful and integrated resources without being besieged by the inherent complexity of the data. Several tools are available which help in visualization of ‘omics’ data on a systems scale like Sungear, MapMan, Genevestigator, Cytoscape, VirtualPlant, REACTOME. Pathway databases are used for modeling systems, since they offer a clear-cut way of building network topologies by the annotated reaction systems. The various pathway databases for systems analyses include KEGG, BioCyc, Aracyc, Pathway Interaction Database (PID) and BioCarta. Also, several comprehensive modelling environments are available, like Gepasi, Virtual Cell, Osprey, Arabidopsis eFP browser, COPASI, R, MatLab and InfoBiotics workbench, E-Cell, Systems Biology WorkBench. The Systems biology model repositories

include Bio-Models database or JWS. Both are public, centralized databases of curated, published, quantitative kinetic models of biochemical and cellular systems. The core systems biology networks include SynBioWave, Cell Illustrator, Moksiskaan, MEMOSys, Babelomics, MetNet, etc.

Conclusion and future perspectives

Plants are a solution to many environmental problems like food and water scarcity in the twenty-first century. Despite the difficulty to find a single perfect resolution, systems biology can be a medium to understand plants through mechanistic efforts and eventually act as a base for partial solutions. The productivity of the individual plants could be enhanced by genetic modifications. However, the comprehensive understanding of the whole plants is a prerequisite to engineer them using molecular approaches. Ample knowledge about the response of the plants to internal and external stimuli is a must which can be gained by systems biology. Investigation of the individual hierarchical biological components and their integration is a key to systems biology. Although, the reductionist molecular approaches are inevitable for expansion of our insight, holistic systems biology approaches provide a complete sense of the plant systems. In addition to the promises, there are some biological and computational challenges to the application of systems' approaches to plants. The difficulty in deciphering the highly complex architecture of plants is one of the major challenges to success of the field. This problem could be dealt by improvement of the current experimental platforms through better technical innovations.

The diversity of the data formats of the experimentally derived datasets is a major computational challenge to the integration of the massive data. Also due to the complexity of the plant biological networks, the experimental testing is not always possible. Still, they can be helpful in assisting and predicting the most promising experimental strategies thereby reducing the labour and time, otherwise used for the 'trial and error' based approach. But the above challenges can be met by the integrative efforts of diverse branches of plant sciences, rather than working in isolation. Hence systems biology will give rise to immense opportunities in decoding the complexity of plants by the fruitful collaboration of the classical plant biologists and computational modelers. The 'unity in diversity' approach of systems biology, is growing and will continue to impact the remarkable future of the plant science, thereby getting the most of the plants' worth to benefit humanity in a pragmatic time frame.

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