

An essential line of inquiry

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We devoted most of our review, ‘Identifying essential genes in *Arabidopsis thaliana*’ [1], not to a detailed discussion of the word essential but rather to the different strategies that have been used to identify genes required for embryo development. Because many of these *EMB* genes are also required for plant viability under standard laboratory conditions and cannot be passed to subsequent generations when disrupted, we thought it was appropriate to designate them as essential, consistent with how that word has been used in genetic studies with other organisms [2–4]. We believe our decision was appropriate, although we agree that a more thoughtful discussion of the concept of essential genes in plants would have been helpful, space permitting. We are not interested in defining genes as either important or unimportant. We did not claim that essential genes are synonymous with the minimal gene set, we do not equate essential with success in the broad sense, and we have definitely not continued to search for essential genes from a mindset ‘in which ensuring a healthy and long life is the goal’. Despite these unfortunate misrepresentations, the commentary by Eran Pichersky [5] raises some interesting questions about what to make of genes that give a loss-of-function phenotype in the embryo. Here is the longer version of how we approached that question several years ago [6]:

Determining what constitutes an essential gene is limited by the absence of a complete collection of null alleles, the variable phenotypes exhibited by loss-of-function mutants, and the ability to rescue some mutants by altering the growth conditions. *Arabidopsis* genes that are required for viability under normal conditions and cannot be passed to subsequent generations when disrupted are often considered to be essential. Problems arise when considering genes such as *LEC1*, where homozygous mutant seeds cannot survive desiccation but give rise to viable plants if germinated precociously, and *EMB* genes with late terminal phenotypes, where mutant embryos may produce callus and germinate to form abnormal seedlings. If we define essential as required to complete the life cycle under normal conditions, then many genes with knockout phenotypes affecting flower development would fall into the essential class despite the absence of reduced viability. We have chosen instead to focus on a more comprehensive dataset of genes that we call indispensable because they give a loss-of-function phenotype of any kind, as detected through visual inspection, cellular characterization, or biochemical analysis under standard or specialized growth conditions. We have divided these indispensable genes into two major groups: those with a phenotype in the embryo, in part because we have an ongoing interest in this developmental

pathway, and those with some other phenotype. Most genes in the first group are required for viability and may therefore be considered essential in the traditional sense. These genes are most comparable to essential genes of microorganisms. Those in the second group are often not required for viability but are needed for a normal phenotype. This classification system enables comparisons to be made with datasets from *C. elegans*, where genes with RNAi phenotypes have been divided into three classes: nonviable, growth defective, and viable with postembryonic phenotypes.

In our review [1], we decided against using the term indispensable because it would have required a more extensive discussion as quoted above. Perhaps that was a mistake. The concept of an indispensable gene in the genetic (not evolutionary) sense is readily defined (discernable knockout phenotype) but not widely used in the literature. By contrast, the concept of an essential gene (knockout phenotype that interferes with viability) is widely understood. Most of the genes cited in our review are essential based on the traditional definition. Some might be more precisely defined as indispensable. We disagree with the contention that establishing a dataset of genes with a loss-of-function phenotype in the embryo (or gametophyte) that cannot be readily transmitted to future generations is a meaningless exercise. If you query the scientific literature at <http://www.ncbi.nlm.nih.gov/> using the intact phrase ‘essential genes’, you will find more than 1500 articles. We do not believe that all of those reports are misguided.

Geneticists have been isolating and characterizing mutants in model organisms for decades with admirable levels of success. Each method of classifying mutants and genes has certain advantages in addition to obvious limitations. Embryo-defective mutants and essential genes of *Arabidopsis* are no exception. The conclusion drawn from countless genetic studies is that some gene knockouts give an obvious phenotype whereas others do not. The question of whether some knockouts might fail to give a phenotype under any circumstance is interesting but also somewhat intractable. We do not claim to understand the biological significance of every gene that fails to give a discernable phenotype under the growth conditions examined to date. But we can draw some valuable conclusions about many of the genes that do.

Sometimes recognizing that a gene is essential in the traditional sense has benefits that are more practical than theoretical. Take for example genes that encode proteins with unknown functions. Many of these genes remain to be analyzed in *Arabidopsis*. By focusing attention on those unknowns that give an obvious knockout phenotype, we can begin to develop useful hypotheses of gene function that would not otherwise be possible. Another example concerns

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the ongoing effort to establish a complete collection of knock-out homozygotes for use throughout the *Arabidopsis* community. By compiling a dataset of genes that fail to give a knockout homozygote because they are essential in the traditional sense, we can help to complete this collection and determine the consequences of disrupting every gene in a model plant. Essential genes can also be of theoretical interest, even to evolutionary biologists. One recent example concerns duplicated genes involved in histidine biosynthesis in *Arabidopsis* [7], including one designated as essential in the SeedGenes database (<http://www.seed-genes.org/>), and their role in the origin of genetic incompatibility and divergent evolution in natural accessions [8]. Would not a comprehensive list of essential genes be valuable in identifying additional cases where a similar isolation mechanism might be involved? Rather than questioning the merits of pursuing a valid genetic approach to the analysis of gene function and dismissing the benefits of employing a term such as essential when analyzing large datasets of genes known to be required for survival in different organisms, we believe it would be more constructive for those with

different perspectives to help integrate the information obtained from a variety of important and, dare we say, essential lines of inquiry to build a more complete understanding of gene function in plants.

References

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Erratum

Corrigendum: Does chromatin remodeling mark systemic acquired resistance?

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In the Review article 'Does chromatin remodeling mark systemic acquired resistance?' by Harrold A. van den Burg and Frank L.W. Takken, which was published in the May 2009 issue of *Trends in Plant Science*, 'H3K4' was incorrectly given as 'H4K4' in three places on page 289. The corrected sentences are below:

Interestingly, expression of *WRKY70* is not only controlled by *NPR1* but also requires histone H3K4 trimethylation (H3K4me3) by *ATX1* (*AtTRITHORAX 1*) [38]. H3K4me3 is also a histone mark associated with transcriptional activation. This change does not affect the proposed model or the conclusions mentioned in the paper. The authors apologize for the error.

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Plant Science Conferences in 2009

International Conference on Retrograde Signalling in Plants

1–3 October, 2009

Berlin, Germany

<http://www2.hu-berlin.de/dfg-forscherguppe804/international-conference/>

Interdrought-III

11–16 October, 2009

Shanghai, China

<http://www.interdrought.org>

9th IPMB Congress

25–30 October, 2009

St Louis, MO, USA

<http://www.ipmb2009.org>