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To cite this article: Sergio Rasmann, Martin De Vos & Georg Jander (2012) Ecological role of transgenerational resistance against biotic threats, *Plant Signaling & Behavior*, 7:4, 447-449, DOI: [10.4161/psb.19525](https://doi.org/10.4161/psb.19525)

To link to this article: <https://doi.org/10.4161/psb.19525>



Published online: 01 Apr 2012.



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Ecological role of transgenerational resistance against biotic threats

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Keywords: plant biotic stresses, adaptation, epigenetic, plant resistance, range expansion, small RNAs

Plants in their natural environments are constantly subjected to biotic stress. In addition to possessing physical barriers and anti-nutritive toxins, plants can be primed to respond more efficiently against future attack via faster and stronger gene activation. Here we discuss recent findings showing that plants can pass signatures of attack to the next generation, thus rendering the progeny more resistant against insect and pathogen attack. A combination of phytohormone signaling, small RNA-mediated gene silencing and DNA methylation are involved in transgenerational induced resistance. Epiallelic variation against biotic threats should be under positive selection in populations of plants where the environment is predictable over time. Similarly, in very genetically homogenous populations, such as during range expansion, epigenome reorganization is a likely mechanism for faster plant adaptation to novel biotic attack. Further research is needed to understand the relative role of the genome vs. the epigenome for the evolution of increased plant resistance.

Plant Immunity Against Biotic Stress

Adaptation to environmental stress is essential for survival and propagation in diverse ecological landscapes. Plants have evolved a large variety of adaptations to counteract herbivore or pathogen pressure, including constitutive physical and chemical barriers,¹ induction of toxic or anti-nutritive proteins or secondary metabolites after attack² and priming for faster and stronger response against future attacks.³ Priming for enhanced responses to subsequent biotic attack has been argued to be relatively cost-free⁴ and is of particular value if plants can predict the future environments to which they, or even their progeny, will be exposed.⁵

Epigenetics of Transgenerational Increased Plant Resistance Against Biotic Stress

Due to the likely role in adaptation, there is an increasing interest in studying the transgenerational inheritance of environmentally induced changes that can confer increased biotic stress tolerance. Such inherited resistance requires epigenetic mechanisms that alter transcriptional activities and can be transmitted through meiosis to subsequent generations.⁶ Three recent studies^{7–9} indicate that epigenetic mechanisms, such as DNA methylation, chromatin remodeling and siRNA synthesis play a central role in regulating transgenerational plant immune responses. Biotic stress from insects and pathogens, as well as plant defense signaling molecules such as jasmonic acid or salicylic acid, can elicit the production of small RNAs (sRNAs)¹⁰ and methylation changes that lead to epiallelic variation in the *Arabidopsis thaliana* (*Arabidopsis*) genome.⁷

Variation in Epigenomic Variability

During the past decade, several studies have reported environmentally triggered acquisition of new, heritable plant traits.^{11–14} In some cases, phenotypic changes could be observed over several generations.^{7,9,11,12,15,16} Analysis of natural accessions and mutant plants shows that there is variation in the acquisition of heritable traits after both biotic and abiotic treatments.^{5,17,18} For example, exposure to physical and chemical stresses in *Arabidopsis* significantly increases somatic homologous recombination numbers, which is related to the expression level of genes involved in homologous recombination and repair.¹⁹ However, in this same study, two subsequent non-treated generations showed low and stochastic increases in somatic homologous recombination that did not correlate with the degree of stimulation in the parental plants.¹⁹ Such results indicate within-species variability in the epigenetic inheritance of resistance traits in plants.¹⁶ Also, at least in the model plant *Arabidopsis*, transgenerational effects are not a general stress response and may require special conditions that cannot be regulated precisely, even in a very controlled laboratory setting.⁹

Merging Epigenetic Variation in Plants with Ecological Research

For plants under biotic attack, epigenetic transgenerational modifications undoubtedly have the potential to increase the ability of progeny to adapt to environmental challenges. This, however, can only be true if environments with threatening biotic factors change less rapidly than the generation time of the plant

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Submitted: 01/30/12; Accepted: 01/30/12
<http://dx.doi.org/10.4161/psb.19525>

that is affected. For instance, in the case of plants with no dormancy period and seeds that germinate next to the parent plant, the maternal environment is a good predictor of the progeny environment. For seeds that overwinter and germinate in the following spring, there may still be predictive value if high herbivore pressure in one year is likely to be followed by large numbers of herbivores in the following year. We thus hypothesize that, across plant species, those with low dispersal will be selected for increased transgenerational epiallele utilization in herbivore resistance compared with highly dispersive species. Additionally, given differential predictive value of the parental environment, it is likely that species expanding into new environments with high and constant threats should be subjected to selection for enhanced stress tolerance at the epigenetic level. Such selection could occur rapidly and should also be reversible if there are changes in the environment. Thus, given the strong plastic responses that a plant can have via heritable epigenetic changes, it is very likely that the epigenome is under natural selection (Fig. 1). However, the extent to which the genome, methylome and transcriptome vary across the natural growth range of different plant species remains to be tested. Investigation of such natural variation in plant epigenetic stress responses will likely be an area of future research. Currently available high-throughput sequencing tools make it possible to dissect the relative importance of genome mutations and rearrangements vs. epigenetic changes. Such studies should include species that have colonized diverse environments, in which populations experience strong ecological gradients and variation in the biotic and abiotic stress conditions. Subsequently, understanding the role of epigenetic processes driving the evolution of plant stress tolerance, and then linking these to plant defensive traits, will offer interesting opportunities for plant breeders. It may be possible to select for epigenetic changes or long-term responses to stress treatments that will provide growers with more resistant crop genotypes that require less energetic and environmentally costly inputs.²⁰

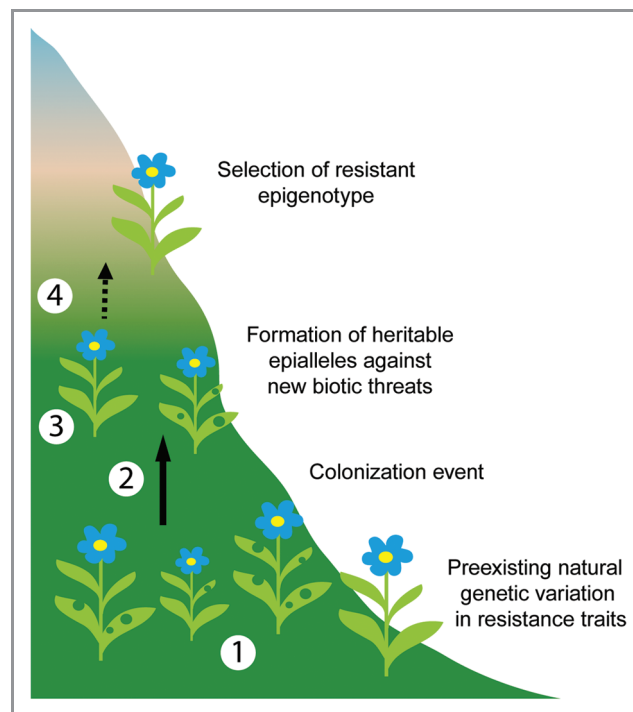


Figure 1. Evolution of plant resistance through alteration of epigenetic regulation. (1) A large natural plant population displaying phenotypic variation in resistance traits due to preexisting natural genetic variation (represented here by variation in the number of leaf holes). (2) Large populations tend to expand into new habitats. In this example, it is expected that alpine plants will colonize higher altitudes due to global climate change. (3) After colonization, new populations with limited and more homogenous genetic diversity will form. When faced with new biotic threats, plants in the novel population will react with a destabilization of epigenetic regulation. Alteration of epigenetic regulation can lead to the formation of heritable epialleles. (4) Epiallelic-driven variation in gene expression generates phenotypic diversity for natural selection to favor more resistant plants. Ideas inspired by Mirouze and Paszkowski.¹⁷

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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