



Review paper

Epigenetics vs Genetics: Unraveling the Importance Beyond the Gene in Natural Forest Populations

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Abstract: Forest trees are complex organisms which nowadays are facing threats under climate change, diseases, insects and pathogens. Their ability to adapt to changing environments depends on their genetic and epigenetic integrity and the relationship between them. The term epigenetics refers to the study of heritable changes in gene expression and function that cannot be explained by changes in DNA sequence. The study of epigenome, at the landscape level may add important acumen in order to identify genomic regions which are associated with adaptive variation. Although population genetic analysis revealed how genetic diversity, structure and linkage can be implemented the significance of variation in epigenetic processes at the population level reveals a composite challenge which remains undetermined. That difference is associated with the inability to associate epialleles with phenotypic variance, whereas for classic genetic analysis, genetic variation can explain a percentage of phenotypic variation. This complex issue has recently become a priority and studies which target genetic and epigenetic diversity were conducted in natural forest tree populations in order to identify the relationship between them and examine additional component of epigenetic diversity in phenotypic variance and plasticity. By estimating epigenetic diversity and especially DNA methylation, improvement of our understanding of the mechanisms underlying natural variation in ecologically important traits will be accomplished. A mini review will be presented in order to enhance our understanding for epigenetic mechanisms in forest tree populations.

Keywords: epigenetic, methylation, forest trees.

1. Introduction

Epigenetics is defined as the molecular mechanisms which are behind the gene and chromosomal stability and produce changes in gene expression without changing DNA sequence. Mechanisms of epigenetics include a) DNA methylation b) Histone modifications (acetylation, phosphorylation, biotinylation etc.), c) chromatin remodeling and d) small RNA (miRNA and siRNA) (Balao et al. 2018; Bossdorf et al. 2008).

Forest trees are complex organisms which contain the larger genomes besides all plant taxa, per example genome size of Norway spruce after complete sequenced was estimated to be 19.6 Gb (Nystedt et al. 2013). Due to their longevity, 300 million years (Myr) for angiosperms and 250-65 Myr for conifers, forest trees had and have to face a series of factors in order to survive and reproduce. Such factors are climate change, pathogens, pest attacks, diseases etc. Their

ability to adapt and survive depends on genetic/epigenetic variation and the relation between them (Avramidou et al. 2015b; Bossdorf et al. 2008; Whipple and Holeski, 2016). Studying epigenetic mechanisms recently became a valuable tool for scientists in order to examine epigenetic inheritance of epialleles and how they contribute to adaptation, plasticity and evolution (Bird, 2002; Bräutigam et al. 2013).

In this paper, a mini review will be presented in order to show the importance of studying epigenetic mechanisms on forest tree species.

2. Epigenetic studies in natural forest populations

According to Richards (2006) there are two possible cases: 1) genetic variation is coupled to epigenetic variation or 2) genetic variation is uncoupled from genetic variation in natural populations. A research was conducted for five natural populations of *Prunus avium* L., an important species for its valuable wood from Avramidou et al. (2015b) with MSAP technique. Results showed that epigenetic variation was uncoupled from genetic variation and most of epigenetic variation resided within populations.

On the other hand, natural populations of *Languncularia racemosa* which is a mangrove tree was studied in two contrasting habitats and exhibited different morphological traits. Epigenetic variation was greater than genetic variation (within and between populations) based to analysis of DNA sequences and methylation patterns (Lira-Medeiros et al. 2010).

Another important study from Raj et al. (2011) examined the important effect of clone history. Cuttings from the same genotype of poplar were sampled from different geographic sites and were grown under the same environmental conditions and drought. The transcriptome and the total DNA methylation reply to water stress was in parallel pathways and were influenced also by geographic origin for two of the three genotypes. These results indicates the importance of the epigenetic memory of genotypes to adaptation (Raj et al. 2011).

Additionally, an interesting paper for *Quercus lobata* (Platt et al. 2015) showed that adaptation is directly linked to CpG methyl polymorphisms which act directly or through linkage to sites under selection. A group of scientists Guggenberger et al. (2016) also investigated those patterns of methylation with climatic variables in the same species. They showed that in *Quercus lobata* CG-SMVs (Single Methylation Variants) explained more overall variance for four climatic variables compared to SNPs and CHG-SMVs or CHH-SMVs (Guggenberger et al. 2016). This results points out the significance of methylation to adaptive evolution or plasticity.

Furthermore, a research has been conducted in natural populations of *Pinus pinea* L. from Sáez-Laguna et al. (2014). According to authors, *Pinus pinea* L. presents low genetic differentiation and high adaptive plasticity, and it is a prominent species for studying epigenetic variation. The collection of genotypes from different Spanish populations, was vegetatively propagated in a common garden and confirmed absence of genetic variability but showed certain differentiation in methylation susceptible markers (Saez Laguna et al. 2014).

3. Epigenetic memory of plants

Recent studies on epigenetic inheritance have already been proved in humans (Genereux et al. 2005), in *Arabidopsis* (Hofmeister et al. 2017; Reinders et al. 2009; Saze et al. 2003) and provided the importance of epigenetic mechanisms in gene regulation, adaptation and evolution. Due to the fact that forest tree species have a long life time period and therefore it is difficult to study epigenetic inheritance, until now few studied have been published.

A group of scientists found in Norway spruce (*Picea abies*) a temperature dependent epigenetic memory from the time of embryo development, which thereafter influences the timing of bud phenology and gene expression (Skrøppa and Johnsen, 2000; Johnsen et al. 2005; Yakovlev et al. 2010). There is therefore an epigenetic memory of climatic conditions in the

embryo during its development in the mother tree. This epigenetic memory influences the subsequent seedling's phenology and performance. The molecular mechanism behind this memory is not yet fully understood but transcriptional changes have been suspected (Johnsen et al. 2009; Yakovlev et al. 2011).

In *Larix kaempferi*, Li et al. (2013) studied the molecular mechanisms which are under the phenomenon of heterosis. By studying DNA sequence variations, changes in methylation status and gene expression, between parental lines and their hybrids, they found that heterotic hybrids presented a lower DNA methylation level than the mid-parent value while non heterotic hybrids had similar level of methylation. Furthermore, in the same study low genomic methylation was found to be correlated with increased gene expression in the heterotic hybrids, and when the transcriptome analyzed from twenty methylated fragments results showed that expression were negatively correlated with DNA methylation status (Li et al. 2013). All those results present the significant role of DNA methylation in the formation of heterosis produced by intraspecific parental lines.

Another epigenetic and genetic inheritance study has been conducted from Avramidou et al. (2015a) in a full sib family of *Cupressus sempervirens* L. in order to estimate how alleles and epi-alleles are being transmitted from parents to offspring. Results showed faithful Mendelian inheritance in a percentage of 71.8% for genetic (AFLP) fragments and low 4.29% for epigenetic (MSAP) fragments. Further, total methylation was higher than the mid-parent value, and also maternal was higher than the paternal. *De novo* methylation appeared in the progeny in a high percentage and positive correlation was found with height (Avramidou et al. 2015a). Results showed the importance of studying DNA methylation in progeny and how epigenetic is associated with growth characteristics of plants.

4. Conclusions and Perspectives

The role of epigenetic mechanisms in forest tree populations have to be studied in details in order to retain information about adaptation, plasticity and phenotypic variation. In the light of upcoming climatic changes forest trees will have to face a variety of diverse environmental stresses. Current research must focus on epigenetic marks and how those will be transmitted in future generations. Until now it has been shown that epigenetic signals is the "quick response" of plants to biotic and abiotic effects (Johannes et al. 2009; Verhoeven et al. 2010), compare to genetic alterations, mutations etc. Epialleles vs genetic alleles proved to react more quickly and stochastically to different stress and evolution (Kalisz and Purugganan, 2004). In quantitative studies epigenetics will also contribute to explanation of genetic and phenotypic variance. From an ecological point of view, ecological epigenetics must be detailed studied in order to find in what extent epigenetics determine the ecological interactions (Bossdorf et al. 2008). According to Richards (2006) the autonomy of epigenetic variation should also be studied, because the majority of developmental mechanisms have a genetic and a epigenetic integral. In the circumstances where epigenetic variation is completely uncoupled from genetic variation is essential to focus in ecological epigenetics (Richards, 2006). Epigenetic mechanisms will continue to gain attention from scientific community in the future in order to understand what is their significant role to adaptation, plasticity and evolution in plants.

5. References

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