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Genetic Diversity, Habitat Fragmentation and Epigenetic Variations

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1. Introduction

There is an increase in the levels in which tropical rainforest and temperate grasslands have become anthropogenically fragmented in recent years. However, an understanding of the genetic and epigenetic mechanisms coupled with conservation biology and biodiversity studies is crucial in explaining habitat fragmentation implications in stable ecosystems (Fahrig, 2003; Henle et al., 2004). The utilization of genetic variability and adaptability can be used as a stepping stone in identifying germplasms that can be used in the search of new ecotypes with novel genes which can be incorporated in crop, fodder and cover tree improvement programs in other similar reclaimable ecological zones. Studies have shown that there is a considerable genetic variability within or between natural populations. This variability provides a genomic flexibility that can be used as a raw material for plant adaptation as pioneer species. There is need to seek for higher genetic variability so as to increase the capacity of an organism to adapt to the ever changing environmental conditions (Ellstrand and Elam, 1993). Low genetic variability has been associated with the inability to cope with abiotic and biotic stresses (Valen, 1965). It is now possible to compare and analyze the pattern and spectrum of genetic variations within or between using molecular genetic tools (Zhang et al., 2009, Madan et al., 2002; Reisch et al., 2005). The amplified fragment length polymorphism (AFLP) is one of the most precise, cost effective polymerase chain reaction (PCR) based ecological tool that has been used for molecular analysis of such population genetic diversity analysis (Vos et al., 1995; Bensch, and Akesson, 2005). It has been shown to be comparatively highly informative, reliable and efficient tool in other grass investigations (Fjellheim and Rognli, 2005). Such tools can be used to determine the correlation between the genetic differentiation and geographic distance among different populations. However, the level of genetic differentiation can be affected by more than one ecological factor in a geographical region, especially environmental heterogeneity (Liu et al., 2004). Other factors could be natural mutation, artificial selection, and combined ecological factors which are instrumental in the differentiation into ecotypes (Liu et al., 2002). Therefore, variations in gene expressions which are caused by abiotic and biotic stresses in the environment trigger epigenetic mechanisms like cytosine DNA methylation which have

recently been used to measure the potential of genome flexibility and intrinsic adaptable evolution mechanisms in dynamic environments. The methylation sensitive amplified polymorphism (MSAP) protocol has been used to combine the genetic diversity studies with epigenetic variation in evaluating the effects of habitat fragmentation especially in plants (Zhang et al., 2009).

2. Genetic differentiation and gene flow

Recent studies have also pinpointed that self-incompatibility can contribute to genetic differentiation especially when coupled with environment habitat selection pressure and low levels of gene flow (Gong et al., 2007). Furthermore, other studies by Liang et al., 2007, showed that wind-mediated dispersal of pollen and seed transport via migrating birds influences gene flow systems and habitat revegetation and could be correlated to artificial selection, habitat selection pressure, environmental heterogeneity, genetic diversity and the eventual differentiation. The occurrence and spectra of gene flow through either seed and/or pollen dispersal was found to possibly be imposing a significant impact on intra- and inter-population genetic variations. The gene flow frequencies between the population pairs were later correlated with the geographical distances (Zhang et al., 2009).

Cluster analysis of the *L. chinensis* also showed that physical barriers like building, mountains and rivers could be instrumental in habitat fragmentation which led to the differentiation and formation of ecotypes due to limitation of gene flow and probable inbreeding alongside an increase in epigenetic variations. Investigations using AFLP in some natural populations of a grass species (*L. chinensis*) identified two easily recognizable phenotypes which had adapted to contrasting ecological habitats due to habitat fragmentation. Some of the phenotypes were in eroded and highly stressful alkaline and saline meadows of pH 8.5 to 9.5 while another was in normal edaphic conditions of pH of less than 8.0 (Zhang et al., 2009, Zhou and Yang, 2003). These genetic and epigenetic variations could have been triggered by the abiotic or biotic stresses. Habitat fragmentation can lead to genetic homogenization among populations; this is because various physical and biological distances usually play a role in determining the level of gene flow and diversity between ecotypes.

3. Inter-clonal genetic diversity

Studies have shown that when levels of gene flow in a population are low, then genetic drift could become the predominant factor in shaping the population genetic structure. This usually results in a within-population homogeneity and causes at the same time an among population differentiation (Reisch et al., 2005). However, with regard to gene flow, for a given plant species, it is most conceivable that causal links with geographic distances, but in some cases it has been shown that there could be little relatedness to geographical distances. This scenario could be envisioned to be caused by multiple other factors which might have imposed their influences on the efficiency or effectiveness of gene flow among populations. Such habitat fragmentation and other physical barriers like mountains, human activities, shielding vegetations and accumulation of valleys could influence the flow of wind and movement of dispersal agents. Further more, recent studies by Li et al., 2009, showed a remarkable observation in their cluster analysis indicating that the soil condition and the proximal distance between the populations have a significant influence in the genetic

diversity analysis. Hence, it is now conceivable that the occurrence and spectra of genetic variations both within a plant population and among populations can be caused by three distinct as well as interlaced factors. These are gene flow through seed dispersal and/or pollen dissemination, genetic drift and habitat induction leading to inter-clonal diversity.

4. Habitat inducement and epigenetic influences in genetic diversity

There is always a possibility of other biologically influenced dispersal factors to influence the enrichment of habitat fragmented clones. These could interfere with wind and pollinator movements (Li et al., 2009) causing homogenization of clones. This possibility was evidenced by an exceptionally low level of gene flow between two populations of *L. chinensis* (Zhang et al., 2009). However, it was clear that physical and/or biological isolation were identified as the most significant factors in causing differentiation of these populations. It was interesting that although habitat heterogeneity like soil pH might not be correlated with genetic variation intrapopulation of the same ecotype, a dendrogram of between these populations constructed by the UPGMA method (Sneath and Sokal, 1973), based on a similarity matrix of AFLP data and calculated according to the Jaccard index showed a close link between the clones grown in the same abiotic conditions (Zhang et al., 2009). Therefore, the possibility of habitat inducement can not be ruled out in causing heterogeneity in stressful abiotic conditions of varied salinity/alkaline which have been known to cause heritable epigenetic variations in plants (Zhang et al., 2010, Kimatu, 2010). Recent studies by Kimatu, 2011, suggested that narrowed genetic base due to inbreeding could contribute to morphological variations and eventually lead to pathogenic attacks to plants. Such eventuality can more be amplified by habitat fragmentation and possible epigenetic variations leading to greater genetic diversity.

5. The impact of anthropogenic destruction of natural habitats

Large continuous natural landscapes are now anthropogenically being destroyed alongside a rapid habitat fragmentation which is a threat to the available biodiversity especially in the tropical forests and temperate grasslands (Young & Clarke 2000, Soulé and Orians 2001). Hence, there has been an increased interest in the assessment of the genetic consequences of habitat fragmentation (Young et al., 1996; Lowe et al., 2005; Ouborg et al., 2006; Honnay & Jacquemyn 2007). Recent studies have established that in contrast to naturally fragmented habitats populations, human impacted fragmented habitats, may suffer from genetic variability erosion as a consequence of isolation and reduced gene flow alongside an increased interpopulation divergence (Zhang et al., 2009, Young, Boyle & Brown 1996). However, many studies have not been done to overrule absolutely that in naturally fragmented landscapes the same phenomenon may not necessarily be occurring. However, some studies have recently shown that not all fragmentation episodes necessarily result in genetic erosion of plant populations (Collevatti et al., 2001; Lowe et al., 2005; Kettle et al., 2007). This isolation can be due to the partitioning of genetic variation among populations and most likely is influenced by the breeding systems and on the reproductive mode of the populations. An increase in clonal propagation may decrease genetic variation within populations although among populations, it might increase genetic differentiation. Adaptations which are triggered by abiotic and biotic stresses in a habitat may increase genetic separation involving epigenetic variations which aid in the formation of epialleles (Liu, 2010).

5.1 Plants in fragmented habitats

Anthropogenic destruction and fragmentation of the formerly continuous natural landscape is increasing and has become now a threat to biodiversity maintenance in ecosystems (Young, Boyle & Brown 1996). The consequences can be the extinction of species and the loss of genetic diversity. What can be the causes of these fragmentations? Some could be caused by abiotic causes like nutrient-poor soils, pH differences, toxicity of some minerals etc. These factors are also known to trigger changes in gene expressions causing epigenetic variations. The smaller the population the more likely it is vulnerable to demographic and environmental stochasticity and genetic erosion (Lande 1988; Menges 2000; Schemske et al., 1994; Young et al., 1996). There has been the phenomenon of formation of 'habitat island' which can be found in natural habitats when they become isolated due to abiotic or biotic fragmentation factors. This is most likely when they are surrounded by non-suitable habitats which could hinder gene flow and genetic variation enrichment (Bossuyt, Honnay & Hermy 2003; Pither, Shore & Kellman 2003; Vucetich et al., 2001). Examples of such habitats can be harsh conditions like infertile soils, occasional high solar radiations, seasonal desiccating winds, steep environments or other biotic impacts like competition from invasive or predatory species. This can decrease population genetic diversity and decrease differentiation among populations. This consequently may increase inbreeding, limited genetic flow due to reduced mate availability (Young et al., 1996). The level of heterozygosity may decrease while it is possible that in the midst of such genetic drift some advantageous genes may be lost, especially if the drift is selective (Lacy 1987). Studies by Barrett & Kohn 1991 and Ellstrand & Elam 1993 showed that in the short term the genetic diversity may reduce plant performance and lower the viability of the seeds from the population. While in the longer term such drifting may result in a limitation for further adaptive evolution mechanism capabilities (Falconer & Mackay 1996).

The differential expression of genes in plants which is regulated by epigenetic mechanisms like cytosine DNA methylation is crucial for phenotypic plasticity in the matching of certain genotypes to variable environments. Studies have shown that although plant growth and reproduction are determined by the genotype and interactions with the abiotic and biotic environment, an increase in environmental variability favours greater levels of plasticity (Schlichting 1986; Sultan 1987). Recent studies by Sumner et al., 2004, who genotyped 411 individuals at nine microsatellite DNA loci found fewer alleles per locus in prickly forest skinks from small rain forest fragments and a lower ratio of allele number to allele size range in forest fragments than in continuous forest. They also found that heterozygosity and variance in allele size did not differ in continuous forests as expected. However, the relationship between genetic (F_{ST}) and geographical distance was significantly stronger for continuous forest sites than for fragments. This is consistent with the disruption of gene flow due to habitat fragmentation. They noted that it is not easy to detect the genetic consequences of recent habitat fragmentation especially if the population size is small and the dispersal rate is not high (Figure 1). This may be influenced by the species dispersal potential, behavioural response and epigenetic flexibility coupled with the ability to adapt to habitat fragmentation limitations (Weins 1997). Therefore, the loss of genetic diversity reduces a population's ability to respond to biotic and abiotic environmental changes hence greatly reducing the chances of evolution and increasing the extinction probabilities (Nason et al. 1997; Booy et al. 2000).

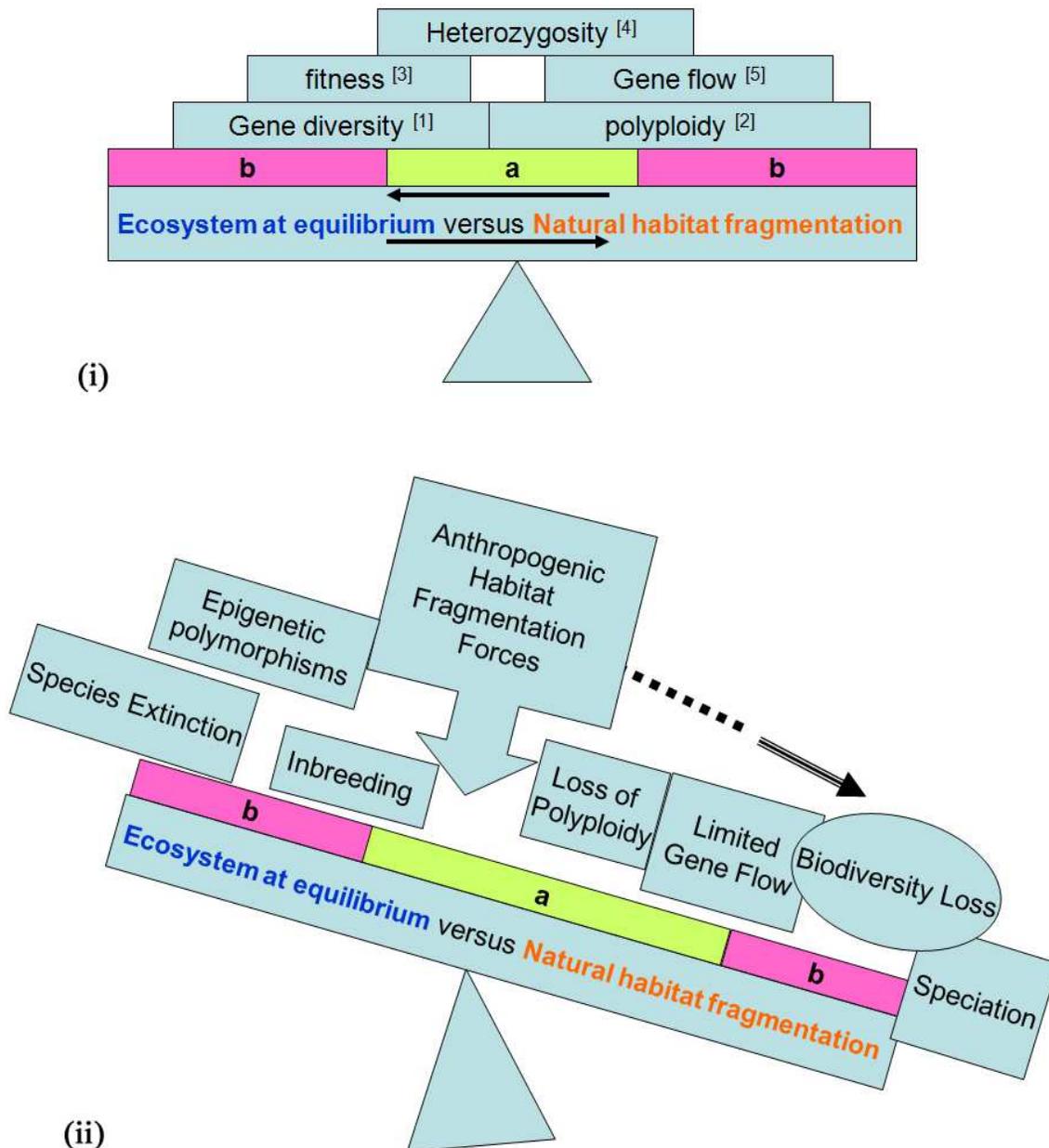


Fig. 1. Natural ecosystems are usually in equilibrium although natural habitat fragmentations are still occurring. This dynamism maintains high biodiversity, gene flow, frequent polyploidy and hybridization events, high fitness etc in the populations (i). Species without narrow geographic distributions (a) are more stable than those with narrow geographical distributions (b). The impact of human activities in natural ecosystems causes habitat fragmentations which cause instability and introduces inbreeding, species extinction and biotic and abiotic triggered epigenetic variations and ecotypes (ii). The references are: [1] and [4]; Lande, 1999; [2], Zhang et al., 2009; [3], Allphin et al., 1998 and [5], Templeton et al., 1990.

5.2 Does habitat fragmentation necessarily affect genetic diversity?

Habitat fragmentation have been found to alters the structure, distribution, and functioning of natural ecosystems (Saunders et al., 1991). This has made many researchers to make the general conclusion that habitat fragmentation definitely affects the genetic diversity. Hence,

many habitat fragmentation studies have been working with the hypothesis that it causes erosion of genetic variability and an increase and interpopulation genetic divergence in plant populations. This could be due to the increase in random genetic drift, inbreeding, and reductions in gene flow (e.g. Young et al., 1996; Sork et al., 1999; Lowe et al., 2005). Furthermore, the genetic diversity and variation of populations is expected to be reduced due to genetic bottlenecks which tend to lower the proportion of polymorphic loci and a reduction in the number of alleles per locus within habitat fragments (Nei et al., 1975; Ellstrand & Elam 1993; Young et al., 1996).

Recent studies by Aguilar et al., 2008, confirmed that indeed there are overall large and negative effects of habitat fragmentation on genetic diversity and outcrossing rates. However, they found that there were no effects on the inbreeding coefficients (F_{IS}). The highest proportion of variation could be explained by the type of mating system, age of the fragment and the rarity status of plant species. They suggested that habitat fragmentation tends to shift mating patterns towards an increased rate of selfing. This can cause an increase in inbreeding and consequently an accumulation of deleterious recessive alleles. This lowers the fecundity of individuals and may in plants, increase seed/seedling mortality, reducing the growth rate of individuals and the eventual diminishing of species or even species extinction (Young et al., 1996). Moreover, the size of the effective population within a fragment and the pattern of genetic variability of the original populations previous to the fragmentation have been shown to be instrumental in determining the immediate effects of habitat fragmentation and the genetic diversity of the organisms in question (Nason et al., 1997; Hamrick, 2004).

Other studied factors which determine the effects of habitat fragmentation are: some particular life-history traits of plants, as is expected to find stronger negative effects on the adult generation of short-lived species compared to long-lived species (Young et al., 1996); vegetative reproduction may also buffer the genetic effects of habitat fragmentation (Honnay & Bossuyt 2005); the mating system has also been implicated in how the genetic diversity can be influenced as cross pollinated generally show a higher genetic variation compared to self pollinating plants (Loveless & Hamrick 1984; Hamrick & Godt 1989); Finally, polyploids are more resistant to the effects on genetic diversity due to fragmentation; (Bever & Felber 1992; Moody et al., 1993). Interestingly, there are now reports which implicate epigenetic variations and their involvement in the adaptation mechanisms of polyploids. For example, it was found that high incidence of alteration in cytosine DNA methylation occurred in allopolyploid plants even in the absence of other structural genomic changes. This suggested that there is an existence of "pure" epigenetic variation which is associated with hybridization and allopolyploidy (Liu et al., 2010). Moreover, it is demonstrated that a recently (less than 150 years) formed natural allopolyploid species, *Spartina anglica*, manifested genome-wide alterations in cytosine DNA methylation which reached a frequency of 35%, and was accompanied by little genetic changes, and which was strikingly hypothesized to be associated with their extraordinary invasiveness in new habitats as a weedy plant (Salmon et al., 2005). Hence, fine-tuned epigenetic states in DNA methylation and histone modifications play critical roles in orchestrating gene expressional trajectories across development and in maintaining genome stability (Liu et al., 2010). Therefore, it is not difficult to imagine that the polyploidy-induced epigenetic alterations will have significant impacts in gene expression, genome integrity and phenotypes even in new abiotic and biotic stresses especially due to habitat fragmentation.

6. Habitat fragmentation and ecology

Because, out crossing plants will be more affected by habitat fragmentation, it is conceivable that, ecological processes like pollination and seed dispersal mechanisms of plants, can have a high impact on genetic connectivity in newly fragmented habitats (Nathan & Muller-Landau 2000; Tewksbury et al., 2002; Hamrick 2004). Hence, the distribution, abundance, composition, and behaviour of pollinator and dispersal organisms will affect the potential of the genetic diversity of the plants in the new habitats (Nason et al., 1997). This is because the attributes of pollinators and seed dispersers are also affected by habitat fragmentation (Aizen & Feinsinger 2003; Griscom et al., 2007). Studies have shown that animal-pollinated and animal seed-dispersed plant species can have decreased genetic connectivity due to habitat fragmentation compared to plants which do not require animals but rely on abiotic factors (Nathan & Muller-Landau 2000 and García et al., 2007).

Studies on tree species have shown that there are their high within-population genetic diversity (0.177) and low genetic diversity among-population differentiation (0.148) for nuclear genes. But, in contrast, annual plants show the opposite (i.e. 0.154 and 0.101 respectively). This suggests a more differentiation for nuclear genes but much less diversity than in trees (Hamrick et al., 1992 and Hamrick and Godt, 1996). Most researchers explain this using the pollen flow hence the gene flow is much higher in trees than in annual plants. However, trees which have been introduced to recolonize temperate and tropical areas have experienced many foundational events, which have led to reduced within-population diversity and increase differentiation due to the narrowing of the genetic base (Kimatu, 2011). There is still need to research on how the pollen flow influences genetic diversity, especially epigenetically. This has its clue on the fact that one key indicator of the pollen flow showed epigenetic gene imprinting in that the paternally inherited chloroplasts showed much less differentiation than maternally inherited mitochondria in pines (Latta and Mitton 1997). Studies have shown that active demethylation, which might be probably acting synergistically with passive loss of methylation, of promoters by the 5-methyl cytosine DNA glycosylase or DEMETER (DME) is required for the uni-parental expression of imprinting genes in endosperm, which is essential for seed viability (Reviewed by Zhang et al., 2010) and most likely lead to habitat influenced genome fragmentation.

7. Molecular diversity and habitat fragmentation

Most studies will easily hypothesize that plant populations in isolated habitats are to a large extent differentiated. However, does population viability in a habitat decrease with a decrease in molecular diversity or is molecular diversity of a population significantly different between contrasting habitats? It could readily be suggested that gene flow among populations is highly dependent on the distance. One general conclusion which is likely to be drawn is that plants from naturally fragmented habitats are more likely to be affected in their genetic diversity level compared to the genetic isolation which is caused by more recent and human induced habitat fragmentation.

How then can we reliably detect the genetic effects of habitat fragmentation which can have genetic and ecologically induced genomic changes? Recent studies using the PCR based amplified fragment length polymorphism (AFLP) showed a higher ability to find habitat fragmentation effects on genetic parameters compared to allozymes. This is because DNA-based genetic markers such as microsatellites have a higher mutation rate, which consequently

causes higher levels of variation and may have higher resolution to detect changes in inter- and intrapopulation genetic variation compared to allozymes. The AFLP (Vos et al., 1995) is a DNA fingerprinting technique that is ideal in resolving genetic diversity among individuals, populations and species (Muller and Wolfenbarger, 1999). It is highly reproducible and polymorphic and can be used to survey overall genetic differences in the nuclear genome in a single assay without any prior sequence knowledge (Vos et al., 1995; Jones et al., 1997). Recently, it has been applied to investigate genetic relationship among species, closely related cultivars and even clones of plants (Mizianty et al., 2006; Yoon et al., 2007; Li et al., 2008; Karimi et al., 2009). Hence, Methylation Sensitive Amplified Polymorphism (MASP) which is a modified version of AFLP may be most suitable in detecting those affected as it combines the genetic diversity evaluation with the epigenetic variation (Zhang et al., 2010).

8. Conclusion

There is an increase in biodiversity study in the last half a decade, due to the opportunities which it offers research scientist and the portfolio of varying characters to the crop and animal breeders. However, the correspondences between genes, alleles and environments on the one hand, and phenotypes on the other have been found to be increasingly complex (Rockman and Kruglyak, 2006). The recent global increases in habitat fragmentations due to natural or human factors have created smaller populations, hereby referred to as species 'islands' from the same population. This process of habitat fragmentation can gradually transform a large population into several smaller islands causing genetic bottlenecks. This transformation can have serious losses in genetic diversity within a population and can result in species extinction. This recent human induced habitat fragmentation may be too recent to be detected genetically. However, variations in gene expressions which can epigenetically be determined can provide important tool in this evaluation. Epigenetic studies have shown that there are variations among individuals in the degree of cytosine DNA methylations of a gene, termed as epialleles. These produce novel phenotypes that are heritable across generations. These epigenetic alleles or epialleles differ at a particular gene sequences. Plants with different epialleles can exhibit distinct phenotypes which are usually mitotically and also sometimes meiotically stable (Kakutani, 2002, Kakutani, et al., 1999). Furthermore, polyploidization has been identified a major evolutionary process where hybridization and chromosome doubling induce enormous genetic and epigenetic variations. Studies of how the specific sequences are restructured are still largely unknown (Liu, 2010). Hence, studies generally seem to point that the number of genes in an organism may not necessarily be used to show the functional complexity of a genome because other factors like abiotic, biotic, genome proteins and epigenetic mechanism are usually acting in harmony to create a unique genetic diversity which can assist in functioning, adaptation and formation of ecotypes.

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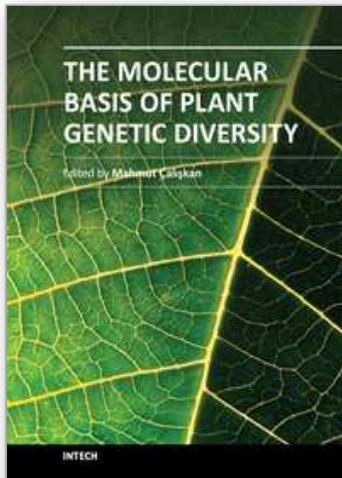
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The Molecular Basis of Plant Genetic Diversity presents chapters revealing the magnitude of genetic variations existing in plant populations. Natural populations contain a considerable genetic variability which provides a genomic flexibility that can be used as a raw material for adaptation to changing environmental conditions. The analysis of genetic diversity provides information about allelic variation at a given locus. The increasing availability of PCR-based molecular markers allows the detailed analyses and evaluation of genetic diversity in plants and also, the detection of genes influencing economically important traits. The purpose of the book is to provide a glimpse into the dynamic process of genetic variation by presenting the thoughts of scientists who are engaged in the generation of new ideas and techniques employed for the assessment of genetic diversity, often from very different perspectives. The book should prove useful to students, researchers, and experts in the area of conservation biology, genetic diversity, and molecular biology.

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