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Review

Consequences of hybridization and heterozygosity on plant vigor and phenotypic stability

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ABSTRACT

The genomic makeup and phenotypes of plants are diversifying, in part due to artificial or natural selection in agricultural and natural environments. Utilization of these variations to enhance crop productivity requires an understanding of the relationships between genotype and phenotype in inbreds and hybrids derived from crosses between these populations. This review highlights recent studies on hybrid vigor (heterosis) and the related phenomenon of hybrid weakness – two types of non-additive inheritance. Heterosis is a phenomenon whereby the phenotype of first-generation hybrids is superior to that of their parents. Intralocus interactions between alleles, complementation of dominant alleles, or inter-loci epistatic interactions are genetic mechanisms that may cause non-additive phenotypic inheritance in hybrids. However, there are different views on what portion of the heterotic variation is modulated by each of these mechanisms. Another aspect of plant vigor is phenotypic stability or robustness in different environments and how this is influenced by gene heterozygosity. Hybrids are not necessarily more phenotypically stable than inbreds since local heterozygosity might be associated with negative effects on biochemical activities. This review integrates genetic and biochemical considerations to illustrate how these relationships may be tightly linked with breeding system and sequence divergence.

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1. Introduction

The radiation of plant populations from one or more centers of origin results in constant changes in their genetic makeup due to natural selection or stochastic events (e.g. genetic drift). A small number of ancestral founder genomes originating from plants growing in one or a few geographic locations have accumulated mutations in parallel to the population's establishment in new niches. These mutations may be selected for or against depending on how they contribute to fitness of the single plant or the population as a whole in new locations. Random neutral mutations can also accumulate in the diversifying genomes over time. Once they have entered the population, these new alleles can be fixed in some or all its individual members, resulting in homozygosity in that locus. Alternatively, more than one allele can remain, resulting in heterozygosity: retention of both alleles might have adaptive value for individuals or the population as a whole. This advantage might be such that each allele contributes to a different component of overall fitness, where these components are normally constrained by a tradeoff relationship, i.e. each of the two alleles is favored due to a positive effect on a different trait. This combination sums to overall higher fitness (see

Abbreviations: QTL, quantitative trait locus; HTL, heterotic trait locus; iCV, index of coefficient of variation.

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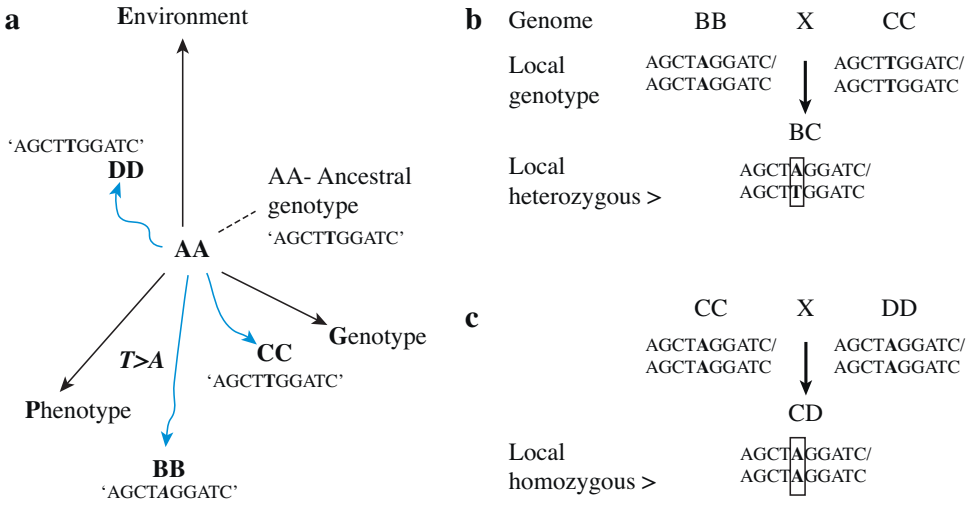

Fig. 1. Radiation and change in plant genetic makeup and its consequences on local heterozygosity of hybrids. (a) An original ancestral genotype 'AA' radiates from a single location to other niches (illustrated as axis E, Environment), and during this time, the genetic makeup (G) and phenotype (P) change. The original representative sequence (AGCTTGGATC/AGCTTGGATC, alleles 1/2) in genome AA mutates at position 5 in genome BB (T > A in italics and bold), and no change occurs in derived genomes CC and DD. (b) Hybridization between genotypes BB and CC, or (c) between CC and DD leads to local heterozygosity or homozygosity at position 5, respectively.

further on). Conversely, the heterozygosity per se could have an advantage under changing environments by achieving, for example, optimal growth at more than one temperature, giving the plant a wider optimal spectrum of activity. This gradual and ongoing genetic change over time is also evident in the evolution of crop plants under domestication. Recent advances in the throughput and depth of resequenced plant genomes are shedding more light on the interplay between allelic diversity and phenotypes that drive adaptation during this process, as well as on the consequences of hybridizing these genotypes. Hybridization between two individuals carrying either different or shared alleles derived from a common ancestor (within-species hybridization) will lead to F_1 hybrids with local heterozygosity or homozygosity, respectively. For example, an original sequence of AGCTTGGATC/AGCTTGGATC (allele 1/allele 2) carried by ancestral genome AA will evolve to AGCTAGGATC/AGCTAGGATC in derived genome BB if it acquires a T > A mutation at position 5. This is compared to no change in derived genomes CC and DD (Fig. 1a). Hybridization between genotypes BB and CC (hybrid BC) will then lead to local heterozygosity in position 5 of this sequence (AGCT***A***GGATC/AGCT***T***GGATC; Fig. 1b), as compared to local homozygosity in the CD hybrid (Fig. 1c).

In this mini-review, I first highlight the relationship between whole-genome hybridization and local heterozygosity with regard to the manifestation of cryptic transgressive phenotypic variation in natural and artificial plant populations. Hybrid vigor is often mentioned with regard to different growth phenotypes which humans are trying to breed for, e.g. hybrids that grow faster to a final larger biomass. The genetic models explained for heterosis are general for any quantitative trait, yet they are relevant to change in the genetic make-up of plant population, or their evolution, only if they increase the fitness or the chances of certain allelic combinations to be inherited to next generations. Plant vigor may also be defined by the stability of the phenotype under different environmental conditions, and heterozygosity can play a positive or negative role in maintaining this stability. Phenotypic stability is derived from harmonious cellular activities, and the basic components of these activities (the enzymes) are organized in complexes with a preference for homo- vs. heterodimers. Therefore, it is conceivable that local heterozygosity due to hybridization of naturally evolved inbreds, as compared to outbreds, will be associated with reduced phenotypic stability.

2. Hybridization: genetic models and possible mechanisms for non-additive inheritance in whole-genome hybrids

Non-additive mode of inheritance is a general phenomenon in which the phenotype of the first generation hybrid could not be simply predicted from performance of both parents, One private case of non-additive inheritance, i.e. heterosis or hybrid vigor, refers to a phenomenon in which whole-genome hybrids originating from crosses within a species exhibit greater biomass, speed of development, or fertility than both parents [1]. On the other hand, hybrid breakdown is a case of non-additive inheritance in which certain hybrid combinations are inferior to both parents. Four genetic models are commonly used to resolve the genetic mechanisms underlying non-additive inheritance. All of these models include interactions of alleles at the same locus or between different genetic loci; dominance, overdominance and underdominance are non-additive intra-locus effects on the phenotype, whereas epistasis is non-additive inter-locus effects on the phenotype.

Dominance is an interaction in which the phenotypic value of the heterozygotes deviates from the expected mean value of the two homozygous genotypes. The distance between the mean phenotypic values of the two homozygous groups equals twice the additive value ('*a*') of the increasing allele for a given locus that includes two alleles [2]. The deviation of the mean value of the heterozygous group from the mid parent value is denoted '*d*'. The dominance-complementation model of heterosis posits that the hybrid will get more genes affecting the trait with d values above zero, than genes that follow an additive mode of inheritance ($d = 0$) and therefore, altogether, its phenotype will deviate from the expected additive value (the "mid parent" value) [3].

Overdominance is the second and most debated genetic model for heterosis and it corresponds to intra-locus interactions; it posits that increased hybrid vigor is the result of positive interactions between two functional alleles that leads to a phenotypic value beyond the range of both homozygous groups. In this case, the dominance value (d) is larger than the additive value (a) of the increasing allele and $d/a > 1$ [4] (see Box). In contrary, if the d value