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Some Conspicuous Traits in Domesticated Rice Oryza Sativa, Due To Recessive Alleles

Review article

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Abstract

Evolutionarily organisms are bestowed with salient morphological features which are considered to be an outcome of activity of functional gene products. However, there are several important features present in organisms owing to recessive alleles in specific gene loci. Interestingly, prevalence of such features due to recessive alleles of gene(s) raises intriguing questions in regard to evolution of the functional alleles in organisms! To have some understanding of this unique phenomenon, we examined four frequently confronted recessive traits in rice plant (*Oryza sativa*) such as (i) fragrance (ii) semi-dwarf height (iii) resistance to pathogens and (iv) non-seed shattering feature and discussed in brief the genetics, biochemistry and evolutionary significance of these traits in rice. These important traits in rice are due to mutations in genes such as *BADH2*, *sd1*, *Xa13* and seed-shattering loci respectively, that otherwise encode essential functional attributes in plant systems. Genes with paralogs possibly attribute to recessive traits through their differential expression patterns. New facts are evolving on role of epigenetic mutations conferring heritable changes in gene expression that are not due to changes in the underlying gene sequence.

Keywords: Green revolution rice; Recessive trait; Resistance to plant-pathogen; Rice fragrance

Introduction

Generally, all observable features in an organism are perceived as functional gene attributes. However, this is not the case always. Interestingly, there are certain features in organisms that are consequences of non-functional genes rather than functional ones. It is difficult to elucidate how non-functional gene contributes toward a feature in an organism. However, there are several examples in nature where non-functional alleles confer distinct traits to organisms. For instance, several features like fruit shape and size, stature of plants, fragrance of seed etc. established in commonly cultivated plants are due to occurrence of non-functional or recessive alleles in their genomes [1-6]. It is noteworthy that prevalence of these kinds of features also has contributed immensely towards their domestication processes [1,7]. The features due to non-functional or recessive alleles follow quantitative mode of inheritance (Figure 1a) and generally do not comply with the dominant mode of inheritance (Figure 1b). Due to recessive or quantitative pattern of inheritance in these traits, identifying them without specific selection procedures is not easy.

In domesticated rice (*O. sativa*), several important traits are known to be due to recessive or non-functional alleles at specific QTLs [3-14]. To be precise, few conspicuous features of *O. sativa* like seed fragrance, semi-dwarf stature, resistance to pathogen etc. have established its significance in agronomy. These qualities are result of mutated or recessive alleles at specific QTLs, coding for nonfunctional protein/enzyme. As a matter of fact, presence of recessive alleles in them doesn't hinder other important characters. Here, we summarize four important conspicuous traits in *O. sativa* that allow them to sustain even in the absence of functional alleles without



Figure 1: (a): A cross between a tall plant (with 7nos leaves) and a dwarf plant (with 3nos leaves) giving rise to F1 generation plant bearing phenotypic features intermediate between both the parent plant i.e. intermediate height and leaf number(5nos). This inheritance pattern follows quantitative mode and differ from typical Mendelian inheritance trend. Generally, polymorphisms at specific QTLs occurring in the genome account for such phenotypic expressions.

(b) A cross between a tall plant (with 7nos leaves) and a dwarf plant (with 3nos leaves) giving rise to F1 generation plant bearing phenotypic features of the tall parent plant (with 7nos leaves) which is the dominant of the two parents. This follows typical Mendelian inheritance pattern.

reduction in their yield.

Rice fragrance

Fragrance is considered an important criterion for determining quality of a particular cereal and also it is used to comprehend a cereal's endemic identity [2,4]. Basmati rice of India and Jasmine rice of Thailand are important because of their distinctive fragrances. Research in this aspect has revealed that fragrance trait in rice is due to a single gene locus on chromosome 8 called fgr [8,9]. A mutation in wild type BADH2 gene of this locus that code for a betaine aldehyde dehydrogenase enzyme results in recessive allele badh2.1. It is believed that the truncated protein product of this recessive allele is unable to catabolize the oxidation of Y-aminobutyraldehyde which is normally catabolized by intact BADH2 protein [15,16]. This defective pathway leads to accumulation of a precursor of the compound 2-acetyl-1-pyrroline (2AP; Figure 2) and thus enhanced synthesis of 2AP. The characteristic fragrance in rice is due to the presence of this compound i.e. 2AP [17,18]. Though there is another isoform of betaine aldehyde dehydrogenase gene in rice (denoted as BADH-1 located in chromosome 4), it plays no role in rice fragrance [19]. Furthermore, fragrance due to 2AP resembles that of pandan (Pandanus amaryllifolius L.) and is exhaled by several other plants such as cucumber (Cucumis sativus L.), aromatic soybean (Glycine max (L.) Merr.), aromatic sorghum (Sorghum bicolor (L.) Moench) etc. [6]. It appears that BADH-2 gene and metabolite 2AP has wide incidence amongst different generas of plants despite their differences at phylogenetic level.

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Green revolution rice

Green revolution rice refers to semi-dwarf rice variety IR8 that was introduced in 1960s as a measure to increased global fooddemand. The characteristic short stature of the rice variety protects them from rain and wind, allowing efficient use of nitrogen fertilizers in them and hence contributes to its yield [3,20,21]. Semi-dwarf trait in IR8 is due to mutation in a gene called *sd1* (semi dwarf). Basically sd1 comprises of two independent alleles located in the chromosome 1 of rice [22]. Wild type *sd1* encodes an oxidase enzyme that metabolizes bio-synthesis of the phyto-hormone gibberellin which in turn determines plant height. This particular enzyme named as GA20 oxidase (GA20ox-2) catalyzes three key conversion steps i.e. $GA_{53} \rightarrow GA_{44} \rightarrow GA_{19} \rightarrow GA_{20}$ (Figure 3) during gibberellin biosynthesis process [3]. A removal of 280 bp within the coding region of this GA200x-2 gene [22] (results in mutation in the sd1 gene). This mutation in turn leads to accumulation of GA₅₃ in the plant there by hindering the conversion process. The mutant plant in experimental conditions was found to be responsive to the externally supplied GA₂₀ suggesting that low level of gibberellin is the cause for this height reduction. In rice, there is another GA oxidase gene coding for GA20 ox-1 enzyme that occur in a different chromosome. Though GA20 ox-1 and GA20 ox-2 are paralogous but their expression varies in different tissues. Therefore, although mutation in GA20 ox-2 affects plant height but do not hinder grain yield in rice [3].

Similar to rice, there is also a green revolution dwarf wheat variety. In case of green revolution wheat, dwarfing condition conferring similar benefit is due to a mutant allele at one of the *Reduced height* -1 loci [23]. Here, mutation leads to a gain-of-function transcription factor that makes the plant unresponsive to Gibberellin hormone and lead to reduced height [23]. The green revolution rice strikingly differ from that of the green revolution wheat both at genetic and biochemical levels. Unlike green revolution rice, dwarfing in wheat





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is due to a semi-dominant gain-of-function mutation at one of the alleles encoding a DNA binding protein determining height of wheat plant.

Resistance to plant pathogen

Plant resistance to incoming pathogen community is mostly governed by gene for gene hypothesis which was proposed by Flor in early 1940s [24]. According to the hypothesis, resistance *in planta* is governed by presence of *R* gene (for resistance) in the plant and an *avr* gene (for avirulence) in the pathogen. Absence of either of the genes or both the genes results in pathogenic condition. The hypothesis is now a proven fact in many plant-pathogen interactions. The gene for gene hypothesis also predicts resistance as a dominant trait. However, there are evidences of plant-resistance being a recessive trait in several plant-pathogen interactions. The first elucidation of plant-resistance as a recessive trait was in barley which is conferred by an allele called *mlo* [25]. The molecular characterization of *mlo* allele suggested that wild type *Mlo* encodes a component that negatively regulates leaf cell death [26].

Interaction amongst rice and its bacterial pathogen *Xanthomonas* oryzae pv oryzae (Xoo) also follows the gene for gene hypothesis. Different *R* genes known in rice are *Xa13*, *Xa17*, *Xa21*, *Xa26* etc. [27,28]. Out of these, resistance due to *Xa13* and *Xa17* are inherited recessively. Recent studies have unveiled role of wild type *Xa13* in transport of sucrose from phloem parenchyma to apoplast region in rice leaves [29]. After gaining entry inside rice leaves, *Xoo* upregulates

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expression of these proteins by manipulating some of its elicitors secreted via type III protein secretion system. An increased level of these proteins ensures constant availability of sucrose inside the xylem and permits the pathogen to survive longer. Likewise, Xa17 encoded protein also transports sucrose to phloem apoplast. In other words, these two genes function paralogously in rice and are named as sweet proteins. Xoo cause disease in rice by deploying a kind of effectors called TALE (transcription activator like effectors) which in turn upregulates Xa13 synthesis. Rice plant harboring mutated Xa13 will be unresponsive to Xoo TALE effectors and thus resistant to disease condition. Similarly, Xoo TALE effectors are also capable of up regulating Xa17 synthesis leading to disease symptoms. Although it is known that Xoo resides in xylem and is able to deploy its type III effectors for regulating gene expression in phloem parenchyma, the mechanism by which the pathogen does it remain to be elucidated. Figure 4 (b) depicts the phenomenon how pathogen entry and induction leads to expression of sweet transporter proteins even in mesophyll cells of leaf. Figure 4 (a) shows the usual extracellular sucrose transport mechanism in the absence of pathogen [30].

In one report corresponding to Xa13, it has been said that the former also has a pivotal role in the pollen development in domesticated rice [31]. Mutations in the promoter region of dominant Xa13 gene lead to down regulated expression that in turn cause recessive state of the gene i.e. xa13. This condition leads to male sterility due to hindered pollen development and simultaneously confers race specific resistance to bacterial blight pathogen [31]. Presence of paralogs possibly compensate for the mutated dominant genes.

Considering the important role of sweet transport proteins akin to Xa13 and other proteins in regulating pathogenesis mechanisms, research in this aspect carries lots of promises. Another xylem resident bacterial pathogen, *Ralstonia solanacearum* has also been shown to derive sucrose from the plant during infection process [32]. Whether



Figure 4a: Schematic representation of the mechanism of sucrose transport from mesophyll cells to sieve element/companion cells in leaf, redrawn after Chen [30]. Sucrose produced photo-synthetically in the mesophyll cells is translocated within cells through the plasmodesmata and then to the phoem parenchyma cells. From phloem parenchyma cells sucrose is transported to extracellular milieu by SWEET sucrose effluxer, which are thought to be present in plasma membrane of the former. Following this, sucrose reaches sieve element/companion cells via an ATPase driven H+-coupled sucrose symporter SUT/SUC [30].



recessive trait for sucrose transport function would have similar impact on *R. solanacearum* pathogenesis too would be an intriguing question in plant-microbe interaction genetics. One stimulating aspect is regarding the adaptability of both of these xylem pathogens. *Xoo* is a foliar pathogen, and *R. solanacearum* invades through root first before spreading to entire plant system through xylem. How, both the pathogens are able to derive sucrose in this environment manipulating their type III protein secretion system elicitors will be an interesting comparative study between these two pathogens for their pathogenesis in near future.

Non seed-shattering trait in rice

Non-seed shattering trait of O. sativa is an important quality that has significantly influenced its domestication processes [33]. Anthropogenic selection of the non-seed shattering rice variety over seed-shattering ones has gradually established the former. Genetic basis of non-seed shattering trait has been connected with a number of QTLs in rice genome such as sh3, sh4, sh6, sh8, qsh1, qsh2, qsh5, ash11, ash12, and sh-h [34-36]. More specifically a QTL sh4 encodes for a transcription factor with varied functionalities [35b,37]. It has been said that an alteration of a single nucleotide from G to T in the sh4 gene locus results in incomplete development and inadequate abscission zone function leading to non-shattering character of O. sativa [35b]. It is not known, if O. sativa possesses a paralog for the same gene function in its genome. However, there is no effect on the productivity of the rice cultivar with this sh4 mutation, similar to other features discussed above. Although, there are different views with respect to the significance of sh4 for the non-shattering feature in rice [38], but, recessive state of sh4 carrying this alteration has certainly been shown to have prominent effect on the non-shattering trait of domesticated rice [35b]. Perhaps, with time, more number of QTLs may be discovered, and it is possible that a cumulative effect of all these QTLs might be necessary for the feature discussed above.

Discussion

Recessive traits discussed here are due to mutations in genes such as *BADH2*, *sd1*, *Xa13* and seed-shattering loci that encodes essential functional ingredients in plant systems. For instance, functional gene products such as betaine aldehyde dehydrogenase facilitate plant's tolerance to stress; GA20_{0x-2} catabolizes gibberellin synthesis, and sweet protein Xa13 is involved in transporting sucrose from photosynthetic to non-photosynthetic tissues via phloem. Seed-shattering locus such as sh4 accounts for proper development of abscission zone between grain and pedicel that renders efficient seed dispersal in wild rice. Nevertheless, non-functional products of mutated states of these genes also exist. Question would arise, then by what means plants counteract mutations in these essential genes? In actuality, plants harbor additional members of these gene families compensating for mutated copies, as is seen in case of rice. In rice, Xa17 serve as an alternative sweet protein like that of Xa13. Same way, $GA20_{oxidase-1}$ functions alike $GA20_{oxidase-2}$, although expressions are tissue-specific. Likewise, BADH1 can compensate for BADH2 functions. The additional copies as mentioned above help the plant to survive and grow normally like their wild type counter parts. Unlike in all other three genes discussed here, paralogs for seed-shattering feature is yet unknown in rice. How the mutations in seed-shaterring loci are counterbalanced in the domesticated rice is an intriguing theme to delve into.

Generally, persistence of recessive traits in domesticated rice varieties retaining high yielding attribute is an un-anticipated occurrence. In case of a rice plant which harbor mutant gene for GA20 $_{\rm oxidase-1}$ may also have short-stature due to intact GA20 $_{\rm oxidase-2}$ activity but its productivity may not resemble with that of Green Revolution rice. These observations may compel us to assume that genes whose paralogs are present in a genome may attribute to recessive traits in the organism through their differential expression patterns. It is axiomatic that due to lethality, recessive traits are not easy to be identified in plants. In this context generation of haploid plants of rice through tissue culture technique is going to be useful in identification of beneficial recessive traits in rice. Ploidy in crop plants is going to be important for recessive traits. For instance, diploidy nature of crops like rice, maize and barley has been shown to be handy in identifying nature of quantitative traits [39-41]. However, genetic analysis in wheat is tricky, due to its hexaploid nature and also comparatively larger genome. This has effected several limitations in studying QTLs in wheat [42,43]. Unlike rice, it is least expected that wheat would have several recessive genes bestowing advantages. But, interestingly, recessive state of gene conferring pathogen resistance in wheat has also been known [44,45]. Pathogen intervened stress may have contributed greatly toward selection and perpetuation of recessive resistance genes in wheat and concurrently anthropogenic selection must have played vital role too. There is another riveting fact about recessive trait. Genes whose recessive state confers distinctive advantages to the host were actually not evolved for such functions. Rather, features due to recessive state of genes could be employed for benefit by the host. For instance evolution of BADH2 was not actually for fragrance neither was Xa13 evolved for protective responses [46,47].

Conclusion

Interestingly, if an organism such as plant can survive, grow and sustain without function of a gene i.e. in absence of a functional gene, then, evolution of that particular gene function or the trait appears to

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be paradoxical! We assume that the functional alleles of these traits were selected in rice during the growth under natural conditions but now due to anthropogenic selection, which is basically a nonnatural mode of selection, rice plant species with traits due to nonfunctional gene(s) have been established. For instance, fragrance in rice might have been deleterious for the plant to survive well as it could invite potential predators of grain and the plant such as insects under natural conditions. Similarly tall rice plants have advantage to grow in low land areas. In the same way, sucrose transporter proteins like Xa13, Xa17 have important role in the rice plant during nutrient-deficient conditions, as these provide sucrose to important and metabolically active regions in the plant! Incidentally, non-seed shattering feature in the domesticated rice gives advantage over shattering ones by allowing for efficient harvesting as well as storage. Unconsciously, mutations in the shattering loci of wild rice varieties helped anthropogenic selection and non-seed shattering feature got established. Furthermore, in due course of evolution, worth of these recessive traits might have been in devising a selection mechanism for giving rise to polymorphic alleles. The selective advantages of these traits imply that the polymorphisms evolved in these genes are in compliance with the selection theory of evolution. In the coming days, we anticipate sufficient evidence for drawing a connection between recessive trait and polymorphism in actuality.

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