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Review

High oleic peanut breeding: Achievements, perspectives, and prospects

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ABSTRACT

Background: The nutritional quality, flavor, and shelf-life of both peanut products and its seeds are dependent on relative quantity of various fatty acids (FAs) like saturated, mono unsaturated fatty acid (MUFA) and poly unsaturated fatty acid (PUFA) present in its oil. High oleic (HO) peanut oils are extremely valued due to its superior nutritional composition for human health and augmented thermo-oxidative stability for industrial purposes.

Scope and approach: From the research perspective, noteworthy progress has been made during last three decades for the development of peanut lines having HO trait in its oil. In this review, the research achievements, perspectives, and prospects of peanut genetic improvement for HO trait is thoroughly discussed.

Key findings and conclusions: The research has helped not only understanding the genetics of HO traits and its genotype (G) by environment (E) interaction but also produced an enormous number of HO line throughout the world. Although, as of now, most of the high O/L cultivars developed are the outcome of traditional breeding efforts. But, with the advent of novel molecular techniques like CAPS and AS-PCR assay for HO peanut breeding program, it is extremely easy to achieve the traits through marker assisted selection (MAS) rather than through either conventional or genetic engineering approaches. The availability of peanut genome sequence and identification of different *ahFAD2* gene families is also expediting the research for the breeding of HO peanut genotypes.

1. Introduction

Consumption of edible vegetable oils at global scale has steadily increased from 87.8 million metric tons (MMT) in the year 2000 to 186.5 MMT in 2016 (USDA-FAS, 2017). This persistent augmentation in demand has been primarily due to the more use of edible oils in various types of food preparations. Nearly 80% of edible oils are derived from various plant species including annual oilseed crops like soybean, rapeseed, sunflower and peanut. Cultivated peanut (*Arachis hypogaea* L.) is an allotetraploid (2n = 4x = 40, AABB) crop which is being cultivated largely by the small and marginal farmers, mostly under low-input situations, in more than 100 countries (Bosamia, Mishra, Thankappan, & Dobaria, 2015; Sarkar, Thankappan, Kumar, Mishra, & Dobaria, 2014). Peanut is one of the major oilseed crops, grown over 25.45 m ha area, contributing to the bulk of total worldwide vegetable oil production (5.77 MMT) (USDA-FAS, 2017).

Peanut oil contains about 12 FAs, of which nearly 80% is composed of oleic acid (C18:1, Δ9) -a MUFA and linoleic acid (C18:2, Δ9, Δ12) -a PUFA. Further, palmitic acid- a saturated FA contributes nearly 10%, while remaining 10% are constituted of up to nine other FAs (Janila et al., 2016). The nutritional quality, flavor, and shelf-life of peanut seeds and its products are contingent on the presence of relative proportion of various FAs like SFAs, MUFAs and PUFAs in its oil (Derbyshire, 2014). The high proportion of linoleic acid in peanut oil is accountable for its low oxidative and frying stability, resulting in rancidity, off-flavors, and short shelf-life of manufactured food products (Mondal, Badigannavar, & Dsouza, 2010). Partially hydrogenated vegetable oils are preferred by the food industry so as to provide ample functionality for a variety of product uses such as high flavor, low-price, and consistent availability (Schwingshackl & Hoffmann, 2012). Numerous chemical and epidemiological studies have shown a strong association between partially hydrogenated fats or trans-FAs and cardiovascular disease risk (Mozaffarian, Katan, Ascherio, Stampfer, & Willet, 2006). Further, during storage, there are breaks in carbon

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double bonds and oxidized lipids produce acids, aldehydes, ketones and hydrocarbons, which are associated with atherosclerosis or hardening and narrowing of the arteries (Cohn, 2002).

Higher oleic acid in any edible oil is highly suitable for a broad range of food-related applications as it has nearly 10-times more auto-oxidative stability over linoleic acid, thus giving longer shelf life to the products (O'Keefe, Wiley, & Knauft, 1993; Pandey et al., 2014). An oleic acid rich diet is a unique approach to reduce systolic blood pressure, thus less risk of heart diseases (Teres et al., 2008). In addition, it also promotes a healthier ratio of high-density lipoprotein (HDL) to low-density lipoprotein (LDL) (O'Byrne, Knauft, & Shireman, 1997), reduces triacylglycerol (Pelkman et al., 2004) and blood glucose levels (Vassiliou et al., 2009).

The function of various edible oil composition in health-related issues is constantly evolving, especially the relation between dietary FA composition and heart diseases (Huth, Fulgoni, & Larson, 2015). Currently, the food processing industries are sensitizing the consumers about the individual FA content of edible oils and other food commodities by way of mass scale advertisements. Thus, HO oil seems an excellent way out for food manufacturers, looking for healthy choice to hydrogenated or saturated oils (Cao et al., 2013a).

For altering the FA composition, concentrated effort has been made in vegetable oil breeding programs, for the identification and generation of HO lines in different oilseed crops including groundnut (Janila et al., 2016), soybean (Haun et al., 2014), and sunflower (Martinez-Rivas, Sperling, Lühs, & Heinz, 2001). The foundation in HO peanut breeding was laid by Norden, Gorbet, Knauft, and Young (1987) who identified the natural HO mutant lines F435-2-1 (79.91%) and 435-2-2 (79.71%) by screening of large number of genotypes from the Gainesville and Marianna locations, respectively. The oleic acid content in these lines was much higher as compared to traditional peanut genotypes having 36–60% (Knauft, Moore, & Gorbet, 1993). This milestone finding suddenly accelerated the HO peanut cultivars breeding programs, especially in USA. In this backdrop, the significant progress made during last three decades in global HO peanut breeding program, and its prospects for further genetic enhancement have been systematically reviewed.

2. Genetics and molecular basis of high oleic (HO) peanuts

2.1. HO trait genetics and cultivar development

A range of genetic control has been reported for HO trait in different genotypes from different parts of the world. Moore and Knauft (1989) reported duplicate recessive genes controlling the HO trait; whereas, recessive digenic and monogenic inheritance were reported for Virginia type and runner type lines, respectively (Knauft et al., 1993). Digenic control of HO was also reported by Lopez, Smith, Senseman, and Rooney (2001) in Spanish-type peanut, but simultaneously speculated the involvement of more allelic variations both within and among the cultivars. Further analysis revealed *ahFAD2* loci exhibiting incomplete dominance, additive and pleiotropic effects for palmitic, oleic and linoleic contents (Barkley, Isleib, Wang, & Pittman, 2013; Isleib, Wilson, & Novitzky, 2006).

Meticulous information about the inheritance of *ahFAD* gene, its background genetic effects and perceptible linkages directed the incorporation of HO trait into elite peanut cultivars. SunOleic 95R was the first HO cultivar released in USA (Gorbet & Knauft, 1997) and so far, more than 90 HO peanut genotypes have been developed worldwide, using traditional breeding, chemically induced mutagenesis and molecular breeding approaches (Table 1). Peanuts having more than 9.0 oleic to linoleic acid ratio (O/L) are classified as 'high oleic' or 'HO' peanuts. These are highly preferred by the shellers, industries, and consumers due to its extended shelf life and several other health benefits (Davis, Sweigart, Price, Dean, & Sanders, 2013). Most of these lines have been developed by the American researchers from Florida State University, NC State University, Georgia State University, Oklahoma State University and USDA-ARS (Table 1). Among Asian countries, China has developed several HO peanut cultivars and countries like Australia, Argentina, South Africa, Israel, Brazil, and Japan are also producing HO peanut products for consumption. Of late, India has also opened its venture of developing HO cultivars (Janila et al., 2016). In addition; chemical-induced mutagenesis breeding approach has also been exploited for the development of a few HO peanut lines. Considerable progress for the development of HO genotypes especially using robust MAS is also in progress (Table 1).

2.2. Characterisation of genes for HO content

PUFAs, which are present in relatively higher proportions in the vegetable oils, are synthesized by membrane-bound fatty acid desaturases (FADs), containing histidine box motifs and conserved membrane-spanning domains (Nakamura, Cheon, Li, & Nara, 2004). FADs introduce double bonds into the hydrocarbon chains of FAs, from a large gene family, and are essential for both lipid metabolism and cell membrane maintenance (Singh, Sinha, & Hader, 2002). The desaturation process takes place in the membranes of plastid and endoplasmic reticulum via two different pathways (Ohlrogge & Browse, 1995). At the sn-2 positions of phosphatidylcholine (PC) (Schwartzbeck et al., 2001), the oleate to linoleate conversion is catalyzed by a microsomal oleate 12-desaturase or *FAD2* (Okuley et al., 1994). Recently, many desaturase genes were cloned and characterized, which has led to the identification of various mutations present in the FAD gene(s) regulating the O/L fluxes in peanuts (Jung, Powell, Moore, & Abbott, 2000; Lopez, Nadaf, Smith, Simpson, & Fritz, 2002; Nawade et al., 2016).

The desaturase activity in peanut are reportedly regulated by two homeologous genes, namely *ahFAD2A* and *ahFAD2B* having 99% sequence similarity (Jung et al., 2000; Lopez, Nadaf, Smith, & Connell, 2000). The open reading frames (ORF) of these genes are devoid of any introns in its coding part which consisted of 1140 bp and encodes 379 amino acids. In *ahFAD2A* gene, a single base substitution mutation at 448 bp position (G448A) resulted in the formation of a missense amino acid asparagine (D150N) from aspartic acid. Whereas, in *ahFAD2B* gene, a single base insertion (A:T) mutation at 442 bp position has resulted in frame-shift mutation and generated a premature stop codon (Jung et al., 2000; Lopez et al., 2000). Wang et al. (2015b) have also identified two natural mutant lines, PI342664 and PI342666 with 80% oleic acid, having G448A substitution mutation in *ahFAD2A* (already known) and C301G in *ahFAD2B* (a novel substitution mutation), resulting in amino acid substitution of D150N and H101D, respectively (Fig. 1). In addition, Patel et al. (2004) reported MITE (miniature inverted-repeat transposable element) insertion in *ahFAD2B* gene of two mutant lines (Mycogen-Flavo and M2-225). Fang et al. (2012) have identified a new mutation in the coding region (C313T) of an EMS mutant peanut line which resulted in an H105Y substitution in its *ahFAD2B* protein. All these *ahFAD2* gene mutations have affected the histidine motifs associated with the metal-ion complex and required for oxygen reduction (Lopez et al., 2000; Yu et al., 2008). Further, the mutations in *FAD2* gene eventually affects its expression, causing poor enzymatic activity and resulting in high O/L ratio in mutant peanut genotypes (Chu, Holbrook, & Ozias-Akins, 2009; Jung et al., 2000).

Using advanced molecular techniques, the O/L trait has been mapped in a RIL population and first QTL, 'TC6H03-TC11A04' was reported for oleic acid (9.7% PVE), linoleic acid (9.0% PVE) and O/L ratio (6.8% PVE) (Sarvamangala, Gowda, & Varshney, 2011). The genotypic effect of *ahFAD2A* and *ahFAD2B* genes explaining nearly 60% of variation in oleic or linoleic acid content was reported by Wang et al. (2013b). Further, Pandey et al. (2014) also identified 78 M-QTLs and 10 E-QTLs for oil-content and oil-quality traits and reported two marker intervals for *ahFAD2A* and *ahFAD2B* genes which are placed on homeologous linkage groups a09, and b09, respectively. Recently, association studies using 268 peanut lines identified three SSR markers