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Peanut (*Arachis hypogaea* L.): A Prospective Legume Crop to Offer Multiple Health Benefits Under Changing Climate

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Abstract: Peanut is a multipurpose oil-seed legume, which offer benefits in many ways. Apart from the peanut plant's beneficial effects on soil quality, peanut seeds are nutritious and medicinally and economically important. In this review, insights into peanut origin and its domestication are provided. Peanut is rich in bioactive components, including phenolics, flavonoids, polyphenols, and resveratrol. In addition, the involvement of peanut in biological nitrogen fixation is highly significant. Recent reports regarding peanut responses and N_2 fixation ability in response to abiotic stresses, including drought, salinity, heat stress, and iron deficiency on calcareous soils, have been incorporated. As a biotechnological note, recent advances in the development of transgenic peanut plants are also highlighted. In this context, regulation of transcriptional factors and gene transfer for the development of stress-tolerant peanut genotypes are of prime importance. Above all, this review signifies the importance of peanut cultivation and human consumption in view of the scenario of changing world climate in order to maintain food security.

Keywords: abiotic stress, bioactive compounds, climate change, legumes, peanut

History of Peanut Origin and Domestication

Peanut (*Arachis hypogaea* L.), or ground nut, is an annual legume grown in tropical and subtropical agro-climatic areas of Asia, Africa, and the Americas (FAO, 2010). Peanut is believed to have originated in South America in the area of Bolivia and Argentina where its domestication started (Bertioli et al., 2011; FAO, 2011; Stalker & Simpson, 1995). A second line of evidence suggested the Incas of Peru as the highly developed ancient agricultural civilization that cultivated it throughout the coastal areas. The Spanish explorers of the New World took peanuts to Spain from where they were distributed by traders to different parts of the world including Asia and Africa (Hammons, Herman, & Stalker, 2016). At present, China, India, the USA, and Argentina are the most notable peanut exporters. Peanut has become one of the major global oil-seed crops cultivated on approximately 26 million ha in about 120 countries yielding about 35 to 40 million tons of peanut pods annually (FAO, 2010; Patel, Mandaliya, Mishra, Dobaria, & Thankappan, 2016; Sarkar et al., 2016). According to FAO, world production is above 45 million tons, averaging about 1.8 t/ha. Peanut production in India is very significant with approximately seven million tons of annual production (Mishra et al., 2015). A major fraction of peanut cultivation is confined to underutilized crop niches of low-income and food-deficit countries and to resource-poor farmers (FAO, 2009). Peanut is also cultivated as a cover crop, forage, green manure, intercrop, and for hay (Langat, Okiror, Ouma, & Gesimba, 2006). Its cultivation improves soil fertility through atmospheric nitrogen fixation (Lal, 2008). There are numerous peanut varieties that are usually preferred on the basis of high fat content, high yield, and low-shelling and high-blanch abilities (Deshpande, Chinnan, & Phillips, 2008; Mulando & Resurreccion, 2006).

Peanut: A Legume to Tackle Food Security Issues

Changing climatic conditions have reduced plant productivity and generated food security issues. In the context of food security and alleviation of hunger, peanut exhibits promising components which make it an exceptional food to meet nutritional needs. Peanut seeds are rich source of multiple vitamins, carbohydrates, proteins, essential fatty acids, minerals, and bioactive compounds of diverse medical importance. These compounds are considered here in some detail.

Nutritional components of peanut and its derived products

Peanut seeds contain carbohydrates (105% to 20%), protein (16% to 36%), and oil (36% to 54%) as major constituents (Davis et al., 2016). They also contain many important functional components including coenzyme Q_{10} (Pravst, Žmitek, & Žmitek, 2010), arginine, and polysterols, which make it a functional food (Akhtar, Khalid, Ahmed, Shahzad, & Suleria, 2014; Francisco & Resurrecion, 2008). Beneficial minerals such as calcium, iron, magnesium, phosphorus, manganese, sodium, potassium, zinc, copper, and selenium are also present in peanuts (Ayoola, Adeyeye, &

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Onawumi, 2012). Apart from these, peanuts are a very rich source of multivitamins including folic acid, thiamine, and tocopherols (Isanga & Zhang, 2007). The antioxidant capacity of peanut is mainly due to the presence of vitamin E, resveratrol, flavonoids, and different hydroxycinnamic acids including caffeic, chlorogenic, coumaric, and ferulic acids (Hasan, Cha, Bajpai, & Baek, 2013; Jonnala, Dunford, & Chenault, 2006; Sales & Resurrection, 2010; Zhang, Sun, Wu, Xu, & Tu, 2017).

Peanut seed oil composition

Peanut is an economically important oil seed crop (El-Akhal et al., 2013; Meena, Meena, & Yadav, 2016) and its seeds are rich sources of dietary essential fatty acids including oleic and linoleic acids (Toomer, 2017). Essential fatty acids, for instance, polyunsaturated omega-3 and omega-6 fatty acids, are synthesized by plants (Qi et al., 2004), and are present in legume crops and soybean in significant quantities (Messina, 1999). Apart from these fatty acids, peanut also contains arachidic and arachidonic, stearic, lignoceric, and behenic acids (Venkatachalam & Kavipriya, 2012). Peanut oil is more saturated than linseed, corn, and cotton seed oils but less saturated than palm and coconut oils and contains 20% saturated and 80% unsaturated fatty acids as mixed acylglycerol (Akhtar et al., 2014). Free fatty acids in peanut oil range between 0.02% and 0.6%. Peanut oil also contains phospholipids including phosphatidylcholine, phosphatidylinositol, phosphatidylethanolamine, and phosphatidylglycerol (Akhtar et al., 2014; Singleton & Stikeleather, 1995). Phospholipids serve as important components of cell membranes (Van Meer, Voelker, & Feigenson, 2008), phosphatidylinositol as a secondary messenger (Vivanco & Sawyers, 2002), and phosphatidylcholine as a neurotransmitter (Blusztajn, Liscovitch, Mauron, Richardson, & Wurtman, 1987). Similarly, phosphatidylethanolamine is reported to be anti-coagulant (van den Besselaar, 1995) and phosphatidylglycerol is recognized as a pulmonary surfactant (Veldhuizen, Nag, Orgeig, & Possmayer, 1998).

The quality and composition of peanut oil varies among genotypes and developmental stages, and in response to environmental factors (Andersen & Gorbet, 2002; Krishna, Singh, Kim, Morya, & Ramteke, 2015). Experimental studies showed that peanut oil with higher oleic acid content exhibited greater oxidative stability, and therefore that peanut oil stability/shelf life is strongly correlated with maturity and oleic acid fraction (Isleib, Pattee, Sanders, Hendrix, & Dean, 2006). For such reasons, peanut genotypes with higher oleic acid fraction have often been used for breeding purposes to develop genotypes with higher oleic to linoleic (O/L) ratios, which are also important for industry (Branch, 2000; Pattee et al., 2002). Limited information is available on the effects of abiotic stresses on seed oil composition. Nonetheless, exposure of peanut plants to drought resulted in a significant reduction in long chain fatty acids and O/L ratios (Hashim, Koehler, Eitenmiller, & Kvien, 1993), and total oil contents (Dwivedi, Nigam, Rao, Singh, & Rao, 1996). Cooler production climate lowers the O/L ratio whereas soils with basic pH and excess Fe-fertigation cause an increase in the O/L ratio in peanut oil (Dwivedi et al., 1993).

An important aspect of the peanut oil is the relative ratios of different fatty acids, which dramatically change with maturity (Pattee, Johns, Singleton, & Sanders, 1974; Sanders, 2002). Typically, a majority of peanut genotypes contain 36% to 67% oleic and 15% to 46% linoleic acid resulting in O/L ratios ranging from 1.19 to 4.46 (Davis et al., 2016; Norden, Gorbet, Knauft, & Young, 1987). Rapid changes taking place in climate can also influence the oil contents and its composition. For example, while studying the oil composition of three different cultivars of peanut, Onemli (2012) observed a significant difference in oil contents of the cultivars in three consecutive years. In addition, high temperature during seed development in 2010 resulted in greater oleic contents than those in 2008 and 2009. In another study with peanuts, Newman et al. (2005) observed that an increase in ambient temperature significantly decreased the peanut nutritive value, but the change in atmospheric CO_2 concentrations (360 and 700 μmol/mol) did not cause a significant effect on the nutritive value. From these studies it can be inferred that high temperature is a more limiting factor for peanut composition than elevated CO_2 concentration.

Other than lipids, peanut oil contains vitamin E as a major antioxidant compound (Jonnala et al., 2006). In plants, this is synthesized within chloroplasts and its concentration varies among different plant parts (DellaPenna, 2005). Typically, its concentration in plant leaf tissues ranges between 10 and 50 μg/g fresh weight, whereas in seeds its concentration can be between 300 and 2,000 μg/g oil (Hess, 1993; Taylor & Barnes, 1981). Nonetheless, variations in the vitamin E concentration in different plant species have been documented (DellaPenna, 2005).

Peanut contains α-tocopherol (48 to 373 μg/mL), β-tocopherol (0 to 140 μg/mL), γ-tocopherol (88 to 389 μg/mL), and δ-tocopherol (0 to 20 μg/mL) with a total vitamin content of 130 to 1300 μg/mL with the absence of tocotrienols (Pattee et al., 2002). Besides vitamin E, peanut also contains vitamins A, B, C, D, and K at significant levels. Other than vitamins, its oil also contains sterols (0.09% to 0.3%) predominantly as β-sitosterol, which exhibits anticancer properties (Awad, Chan, Downie, & Fink, 2000). In short, peanut oil is a multifunctional source of essential fatty acids and vitamins. Some of the major nutritional components are presented in Table 1.

Bioactive Compounds Make Peanut a Functional Food

The copresence of multinutrients and bioactive compounds in peanut seed contributes to its nutraceutical properties (Figure 1). Peanut seeds and peanut food products are rich sources of arginine which has been considered as a semi-essential amino acid (Tapiero, Mathe, Couvreur, & Tew, 2002). In peanuts, its concentration ranges between 8.6 and 23.5 μg/g seeds (Aninbon et al., 2017; Young & Mason, 1972). Arginine acts as a precursor of agmatine, glutamate, nitric oxide (NO), proline, and polyamines (Guoyao & Morris, 1998). The consumption of arginine protects against gastro-intestinal tract problems and is also involved in the spermatogenesis and muscular activity, and has antiaging effects (Duggan, Gannon, & Walker, 2002). Other important food legumes with significant nutritional components include lentils, cowpea, chickpea, and green pea, and the detailed profile of nutritional components in them has been reported (Iqbal, Khalil, Ateeq, & Khan, 2006).

Peanut seeds also contain phytosterols in significant quantities, which contribute to health beneficial effects. In plants, phytosterols or stanol esters may frequently occur in plant cell membranes (Arya, Salve, & Chauhan, 2016). Phytosterols present in peanuts are 80% β-sitosterol, 10% campesterol, and 5% stigmasterol (Jonnala et al., 2006). Plant sterols or phytosterols mimic cholesterol both in structure and function. However, when ingested in the human body, they compete with low-density lipoprotein-cholesterol (Cedó et al., 2017; Moruisi, Oosthuizen, & Opperman, 2006; Rudkowska, AbuMweis, Nicolle, & Jones, 2008), resulting in subsequent reduction in blood LDL-cholestrol levels inside blood vessels (Ostlund, 2002;

Table 1—–Nutritional chemistry of peanuts seeds.

No.	Nutritional chemistry	Quantity	Reference
1	Trans-Resveratrol	98 μg/mg	Medina-Bolivar et al., 2007
2	Edible oil	43% to 55%	Reddy, Reddy, and Anbumozhi, 2003
3	Fat	38% to 50%	Zhao, Chen, and Du, 2012
4	Palmitic acid (C16:0)	9.3% to 13.0%	Carrin and Carelli, 2010
5	Oleic acid (C18:1)	35.6% to 58.3%	Carrin and Carelli, 2010
6.	Linoleic acid (C18:2)	20.9% to 43.2%	Carrin and Carelli, 2010
7	Stearic acid (C18:0)	1.1% to 3.6%	Grosso, Lamarque, Maestri, Zygadlo, and Guzmán, 1994
8	Arachidic acid (C20:0)	0.3% to 2.4%	Grosso et al., 1994
9	Eico-senoic acid (C20:1)	0.7% to 3.2%	Grosso et al., 1994
10	Behenic acid (C22:0)	1.8% to 4.4%	Grosso et al., 1994
11	Lignoceric acid (C24:0)	0.4% to 1.9%	Grosso et al., 1994
12	Crude protein content	22% to 30%	Sebei, Gnouma, Herchi, Sakouhi, and Boukhchina, 2013
13	Carbohydrates	1.51 g/100 g	USDA, Food Composition Data-base, 2017
14	Oligosaccharides	18%	Tharanathan, Wankhede, and Rao, 1975
15.	Starch	12.5%	Tharanathan et al., 1975
16	Hemicellulose A	0.5%	Tharanathan et al., 1975
17	Hemicellulose B	3.5%	Tharanathan et al., 1975
18	Cellulose (fiber)	4.5%	Tharanathan et al., 1975

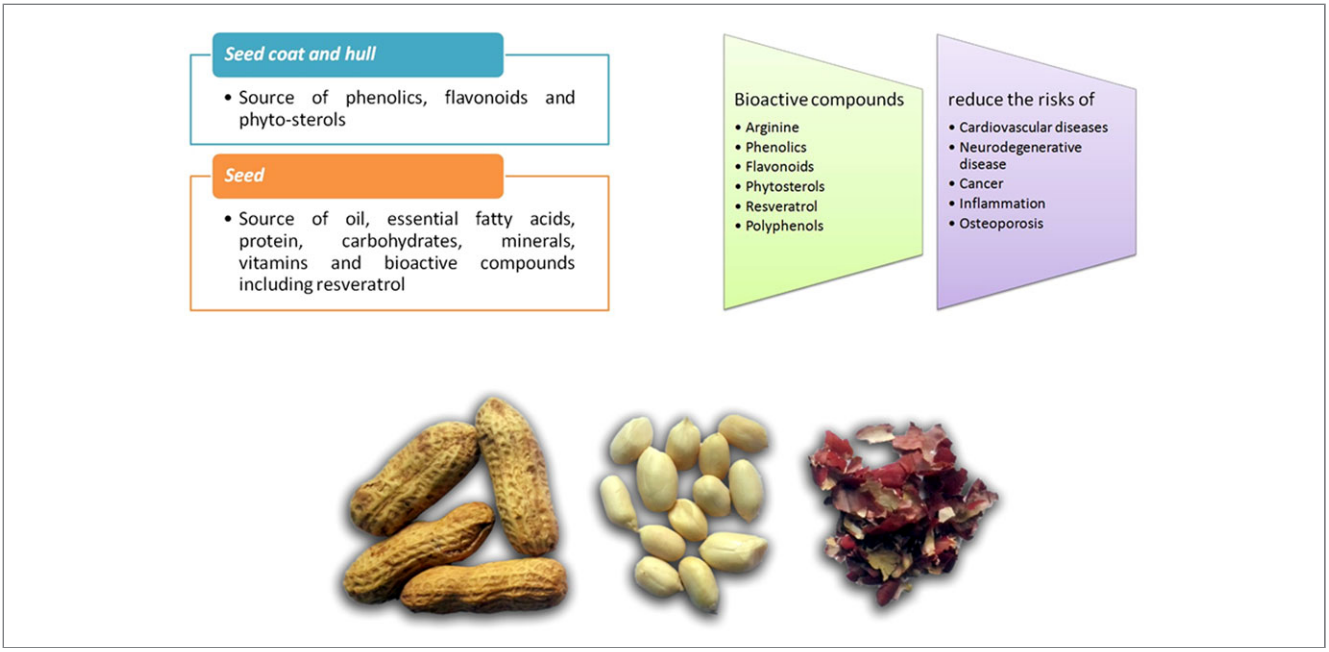


Figure 1–An overview of different bioactive compounds in peanut.

Varady, Houweling, & Jones, 2007). Apart from this, phytosterols exhibit strong antitumor properties and can decrease the development of different types of cancer cells (De Stefani et al., 2000; Ju, Clausen, Allred, Almada, & Helferich, 2004; McCann, Freudenheim, Marshall, & Graham, 2003; Mendilaharsu, De Stefani, Deneo-Pellegrini, Carzoglio, & Ronco, 1998). For example, addition of β-sitosterols to the culture of human cells induced apoptosis in different cancerous cells (Awad, Chinnam, Fink, & Bradford, 2007; Choi et al., 2003; von Holtz, Fink, & Awad, 1998).

Peanut seeds, skin, and derived products contain phenolic compounds in significant quantities, which contribute to prominent antioxidant capacity (de Camargo et al., 2017; Sales & Resurreccion, 2010; Tedesco, Monaco-Lourenço, & Carvalho, 2017). Enhanced production of phenolic acids was reported in peanut plants during early growth stages (Sobolev, Horn, Potter, Deyrup, & Gloer, 2006), and/or in plants exposed to various microbial elicitors (Devi & Reddy, 2002; Sobolev, 2013). Numerous studies report the presence of significant amounts of biologically important phenolics (resveratrol, flavonoids, and polyphenols) in peanuts and related products. Among these, resveratrol (3,4′, 5-trihydroxystilbene) is a phytoalexin and a member of the stilbene family of phenolic compounds produced by different plants including peanuts (Ingham, 1976). Resveratrol is present in almost all parts of peanuts including shell, seeds, skin, and derived products (Sanders, McMichael, & Hendrix, 2000; Sobolev, 2013; Sobolev & Cole, 1999; Wang et al., 2005). The resveratrol fraction in peanut edible products is directly linked with its concentration in the peanut kernels (Yu, Liu, Shi, Liu, & Wang, 2015). Interestingly, resveratrol contents vary significantly depending upon cultivar, development stage of peanut, and prevalent environmental conditions (Hasan et al., 2013). Resveratrol contents have been reported to increase among peanut plants in response to stress conditions including injuries or pathogen attack (Giovinazzo, Ingrosso, Paradiso, De Gara, & Santino, 2012) Exposure of peanut plants to UV and ultrasound treatments increased the resveratrol contents in their seeds (Ku, Chang, Cheng, & Lien, 2005; Yu et al., 2015). This increase was linked with increase in the activity of phenylalanine-ammonia lyase and improved plant defense responses. In addition, by using elicitors or exposing peanuts to stress, the resveratrol fraction can be increased (Rudolf & Resurreccion, 2006). An increase in the resveratrol content in peanut sprouts was evident on the 10th day after germination (Wang et al., 2005). Stillbene-derived compounds have become increasingly popular among scientists worldwide due to their anti-cancer (Brown et al., 2010), neuro-protective (Sun, Wang, Simonyi, & Sun, 2010), anti-inflammatory (Capiralla et al., 2012), cardio-protective (Qin et al., 2012), antidiabetic (Sharma, Chopra, & Kulkarni, 2007), and antidepression effects (Pathak, Agrawal, & Dhir, 2013), and other diverse therapeutic roles within biological systems (Baur & Sinclair, 2006). Resveratrol mitigates the aging of skin by suppressing aging related genes (Lephart, Sommerfeldt, & Andrus, 2014). Furthermore, resveratrol appears to extend the life cycle of fruit flies (*Drosophila melanogaster*), yeast (*Saccharomyces cerevisiae*), and laboratory mice (Baur et al., 2006).

Peanuts are also a rich source of flavonoids including polyphenols (Crozier, Jaganath, & Clifford, 2009; Lou et al., 2004). Flavonoids play important roles in plants including plant–herbivore interactions (Renwick, Zhang, Haribal, Attygalle, & Lopez, 2001; Simmonds, 2001) and defensive mechanisms, and also help in pollination (Harborne, 2001). A significant amount of quercetin (133 to 289 μg/g), a major bioflavonoid, has been reported in peanut seeds (Wang et al., 2008). The flavonoid fraction in the peanut seeds varies significantly because of genetic variability among peanut genotypes (Mondal, Phadke, & Badigannavar, 2015). The polyphenol content in dried peanut skin ranges from 90 to 125 mg/g (Nepote, Mestrallet, & Grosso, 2004; Shem-Tov et al., 2011). Other than peanut seeds and seed coat, a significant fraction of flavonoids has been reported in peanut hull (Zhang et al., 2017). Moreover, peanut derived products contain a prominent flavonoid fraction (de Camargo et al., 2017). Flavonoids protect vitamins, lipids, and various enzymes from oxidative damage and inhibit the action of enzymes that produce reactive oxygen species (ROS) (Brown, Khodr, Hider, & Rice-Evans, 1998; Kelly, Anthony, & Dennis, 2002; Pandey et al., 2012). Likewise, many other phenolics and flavonoids impart multiple health promoting benefits (Guerrero et al., 2005; Ren, Qiao, Wang, Zhu, & Zhang, 2003; Spencer, Vauzour, & Rendeiro, 2009; Tunon et al., 2009). Overall, peanut pods are a very rich source of flavonoids which contribute to their strong bioactive potential.

Peanut Responses to Abiotic Stresses

Legumes are a significant source of plant-based proteins in the diet for humans and livestock, and there is a need to improve abiotic stress tolerance under the changing climate (Araújo et al., 2015). Keeping in view the higher nutritional, medicinal, and commercial value of peanut and its products, improving response of peanut varieties to environmental stresses is an important goal (Sarkar, Thankappan, Kumar, Mishra, & Dobaria, 2016). A brief account of peanut responses to environmental stresses is provided.

Drought

In the tropical and subtropical regions, peanut is cultivated under rain-fed conditions by resource poor farmers where it is exposed to abiotic stresses such as drought and salinity (Bhauso et al., 2014; Sarkar et al., 2014). A major part of global peanut cultivation takes place in areas exposed to water shortage. Over six million tons annual loss of productivity of this important oil-seed crop occur due to drought (Bhatnagar-Mathur et al., 2013; Gautami et al., 2011).

The drought mediated losses in the peanut production is due to several reasons. Peanut plants bear aerial flowers and, after pollination, the fertilized ovaries develop into gynophores or pegs (Haro, Mantese, & Otegui, 2011). The peg is a positively geotropic stalk-like structure containing embryos in which basal cells of the fertilized ovary elongate (Jacobs, 1947). Pro-embryo development is required for the elongation of pegs, which initiate penetration into the top-soil layer (Periasamy & Sampoornam, 1984). This phenomenon is termed as pegging and occurs when the initial pegs attain a length of 3 to 4 mm (Ziv, 1981). Under sufficient water availability, pegging is a fast process (Haro, Dardanelli, Otegui, & Collino, 2008), and the pod growth initiates after this phase resulting in subterranean fruits (Periasamy & Sampoornam, 1984; Smith, 1950).

Drought mediated increase in top soil hardness can restrict or delay peg penetration into the soil and therefore restrict the pegging stage resulting in limited pod set and subsequent seed numbers (Haro, Dardanelli, Otegui, & Collino, 2010, 2011). However, in contrast, if the drought affected pegs are re-watered, viable pegs starts penetrating the soil again (Haro et al., 2008). The resumption of pegging upon re-watering is an adaptive trait in peanut plants that ensures long-term survival of the fertilized embryo compared with other grain-crops like maize and soybean where embryo viability is rapidly lost (Westgate & Boyer, 1986). Overall, drought is the major abiotic stress-limiting peanut crop yield (Boote, Varnell, & Duncan, 1976; Haro et al., 2008). Furthermore, owing to a lack of genotypic variability for better water use efficiency among peanut plants (Gautami et al., 2011), the development of drought-tolerant peanut genotypes is a major focus of plant breeders (Sarkar et al., 2016).

Salinity

Like other legumes, peanut plants are susceptible to soil salinity (Greenway & Munns, 1980) and genotypic difference for salinity tolerance exists within the species (Sun, Hu, Shen, & Zhang, 2013). Peanut plants are glycophytes indicating their vulnerability to highly saline soils (Banjara, Zhu, Shen, Payton, & Zhang, 2012). In this context, marked salinity-mediated reduction in the peanut pod production has been reported (Meena et al., 2016). Salinity can reduce peanut seed germination, seedling establishment, and the dry weight of plants (Meena et al., 2016; Parida & Jha, 2013). Moreover, salinity induced disruption in the photosynthetic apparatus and disturbance in nutrient uptake are believed to contribute to peanut yield losses (Qin et al., 2011a). Salinity induced downregulation of genes associated with photosynthetic light harvesting complex proteins and phenylalanine metabolism, and subsequent production of terpenoids, phenylalanine, tyrosine, and plant hormones has been reported (Chen et al., 2016). At the molecular level, salinity induced downregulation of 36 peanut genes along with upregulation of seven genes associated with the ROS network after 48 hr of salinity treatment has been reported (Chen et al., 2016). Efforts are required to develop salt tolerant peanut genotypes using transgenic approaches (Chen et al., 2010) so as to increase the yield of cultivated peanut. The use of good quality seed and salinity management practices could contribute to improvement in peanut yield under salinity stress (Meena et al., 2016).

Heat stress

The cultivation of peanut is largely confined to warmer regions of the globe (Selvaraj et al., 2011). However, in such regions, water stress in combination with heat stress (HS) poses a serious threat to crop production. Peanut growth is best favored at optimum temperatures ranging between 25 and 30 °C and the pod yield substantially decreases when temperature exceeds 33 °C (Prasad, Boote, Hartwell, & Thomas, 2003). Therefore, HS disturbs plant growth and development resulting in considerable peanut productivity losses (Gillooly, Brown, West, Savage, & Charnov, 2001). In some reports, HS negatively influenced physio-biochemical processes in peanut genotypes affecting dry mater partitioning, fruit set, and overall yield (Srinivasan, Takeda, & Senboku, 1996; Vara Prasad, Craufurd, Kakani, Wheeler, & Boote, 2001). Several studies reported genotypic variation for HS tolerance among peanut genotypes (Awal, Ikeda, & Itoh, 2003; Prasad et al., 2003; Selvaraj et al., 2011; Vu, 2005). To provide for future needs, breeders have focused on screening/developing HS tolerant peanut genotypes.

Iron deficiency

Iron (Fe) is the fourth most naturally occurring element in the Earth's crust and its involvement in plant growth was recognized very early (Ding et al., 2010). However, in soils with higher pH and bicarbonates, it is precipitated in the form of insoluble Fe^{3+} oxides reducing Fe availability despite its relative abundance in soils (Song et al., 2016). Fe-deficiency is a major problem for dicotyledonous plants and other crops growing in calcareous and alkaline soils resulting in leaf chlorosis through inhibition of chlorophyll synthesis (Ding et al., 2010; Zhang et al., 2012). Fe-deficiency interferes with aminolevulinic acid (the pre-cursor of chlorophyll) formation (Pushnik & Miller, 1989), cellular enzymatic reactions and, most importantly, the photosynthetic electron transport chain (Marschner, 1995). Iron deficiency chlorosis commonly affects higher plants cultivated on calcareous soils. Chlorophyll content has been used as an indicator of Fe-status in plants (Graziano, Beligni, & Lamattina, 2002).

A significant fraction of peanut crops cultivated on calcareous soils in Northern China exhibited symptoms of leaf chlorosis due to Fe-deficiency resulting in about one third of oil-seed productivity losses (Kong, Dong, Xu, Liu, & Bai, 2014; Zuo, Zhang, Li, & Cao, 2000; 2007). Peanut is a strategy-I plant that is vulnerable to Fe-deficiency on calcareous soils (Song et al., 2016). Under such conditions, peanut plants respond to Fe-insufficiency in a three-step process characteristic of strategy-I plants (Marschner, Róheld, & Kissel, 1987; Santi & Schmidt, 2009). In strategy-1 plants, the first step is rhizosphere acidification that increases Fe^{3+} solubility (Palmgren & Harper, 1999; Santi & Schmidt, 2009). This is followed by catalytic reduction of Fe^{3+} chelate to Fe^{2+} by ferric chelate reductase (Ding et al., 2009; Robinson, Procter, Connolly, & Guerinot, 1999) and a third step of iron uptake by plasmalemma IRT1 (metal transporter) also termed as Fe-regulated transporter in root cells (Ding et al., 2010; Eide, Broderius, Fett, & Guerinot, 1996). Recently, it has been reported that the exogenous application of salicylic acid, sodium nitroprusside, and epibrassinolide ameliorated Fe-deficiency in peanut (Dong et al., 2016; Song et al., 2016). Furthermore, drainage of the calcareous soils improved Fe-availability (Zuo, Ren, Zhang, & Jiang, 2007).

Influence of Abiotic Stresses on Peanut N_2-Fixation

It is estimated that biological nitrogen fixation (BNF) by legumes annually adds 40 million tons of N to soils (Herridge, Peoples, & Boddey, 2008). Peanut, like other legumes, improves the soil nitrogen status of soil due to its ability to obtain fixed nitrogen from bacterial symbiosis (Furlan, Bianucci, Castro, & Dietz, 2017; Graham & Vance, 2003). More specifically, peanut exhibits a substantial N_2-fixation ability which is nearly 100 to 190 kg N/ha (Boddey, Urquiaga, Neves, Suhet, & Peres, 1990). Peanut cultivation contributes to sustainable agriculture (Lal, 2008). Abiotic stresses including drought, salinity and Fe-unavailability interfere with the N_2-fixation ability of peanut and other legumes. Water unavailability to peanut plants resulted in a significant reduction in N_2-fixation, although its magnitude varied among cultivars (Furlan et al., 2017). Drought induced reduction in BNF is believed to be due to inadequate oxygen, water supply, carbon and nitrogen imbalance, and impairment of sucrose synthetase activity (Furlan et al., 2017; González, Gordon, James, & Arrese-Igor, 1995, 1998; Serraj, Bona, Purcell, & Sinclair, 1997). Salinity also impairs BNF by reducing rhizobia viability and nodule growth attributes such as nodule number, size and dry weight (Dardanelli et al., 2009; Fabra et al., 2010). A marked reduction in the BNF of peanut plants under salinity has been attributed to salt-induced inhibition of nitrogenase activity (El-Akhal, Rincón, Coba de la Peña, Lucas, & El Mourabit, 2013). Other than salinity, iron deficiency also negatively affects the BNF ability of peanut plants and other legumes. Improved Fe status of the peanut plants contributed to improve BNF (Guo et al., 2014). Fe is essentially required for the legume-rhizobium symbiosis (Brear, Day, & Smith, 2013; Terry, Hartzook, Jolley, & Brown, 1988), nitrogenase and leghemoglobin (Ragland & Theil, 1993). In short, peanut cultivation improves soil N status, whereas abiotic stresses impair peanut BNF ability to a considerable extent.

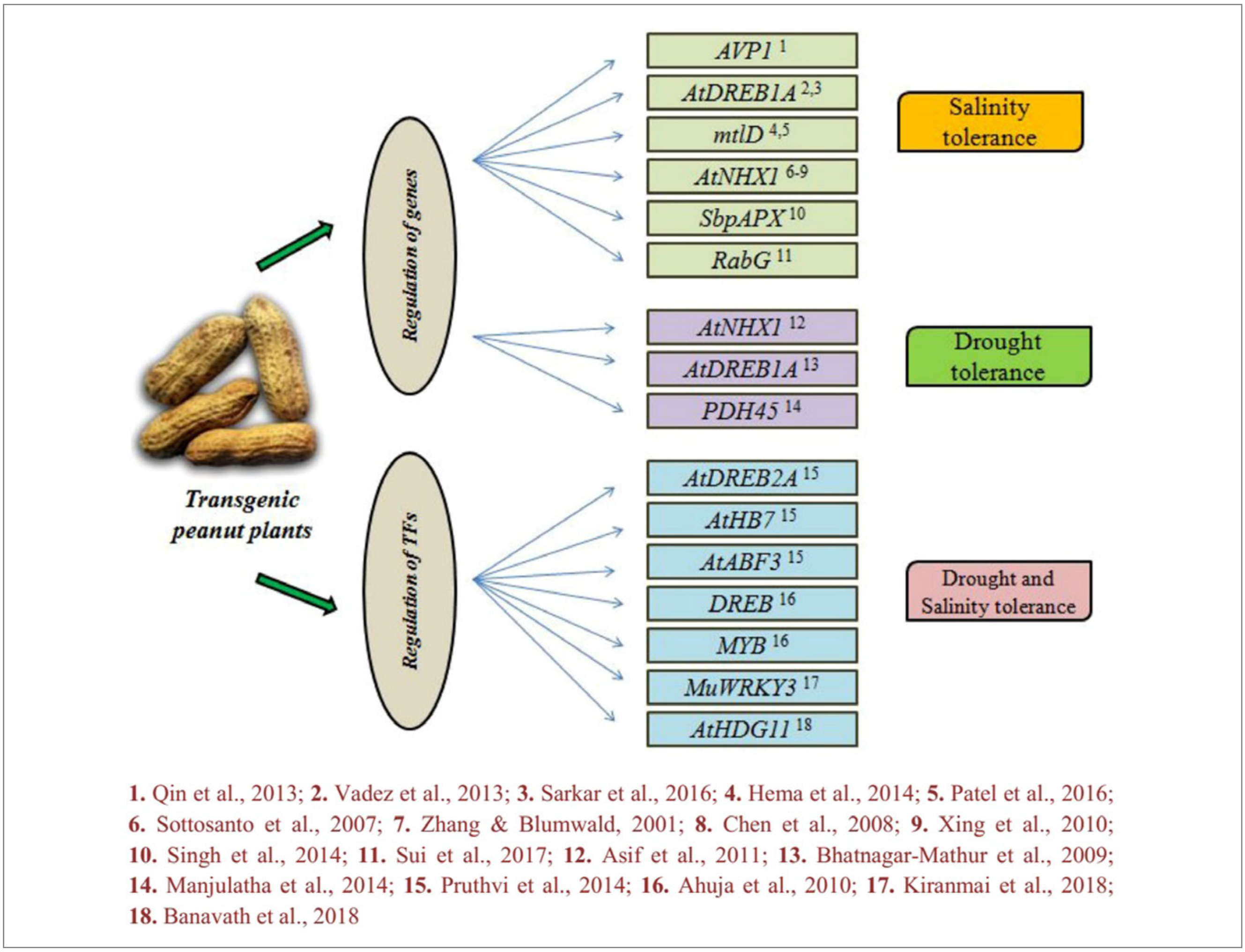
Biotechnological Approaches for Improving Abiotic Stress Tolerance in Peanut

Biotechnological approaches have enabled researchers to identify genetic resources and the manipulation of these resources for the development of transgenic stress tolerant crops. Advances in genomics and genetic engineering for cultivated peanut improvement have been reported in some comprehensive detailed reviews (Krishna et al., 2015; Pandey et al., 2012). Some of the important components of these approaches are discussed here.

Insights into transgenic peanut plants

The past decade has seen the development and use of transgenic plants as an important approach to modify and enable crops to withstand variable and ever-changing climatic conditions (Ahanger et al., 2017). In this context, transgenic approaches have been regarded as very effective for the induction of salt and drought tolerance among peanut plants so as to achieve improved yields (Krishna et al., 2015; Pandey et al., 2012; Pruthvi, Rama, Govind, & Nataraja, 2013, 2014; Sarkar et al., 2014). Apart from these reports, transgenic peanut plants exhibited higher activities of enzymatic antioxidants that contributed to oxidative stress regulation (Pandurangaiah et al., 2014). Consistent with these reports, the over-expression of *AtNAC2* gene in peanut conferred abiotic stress tolerance (Patil et al., 2014).

Salinity tolerance. Salinity mediated reduction in the physio-biochemical processes of several crops under salinity has been reported earlier and there is a need to develop/ identify salt resistant plants (Daliakopoulos et al., 2016; Negrão, Schmöckel, & Tester, 2017; Roy, Negrão, & Tester, 2014). For peanut, a number of genes associated with abiotic tolerance have been identified (Figure 2) indicating a potential for the development of transgenic plants for abiotic stress tolerance including drought and salinity (Saravanakumar & Samiyappan, 2007; Zhao et al., 2013). Recently, a transcription map of peanut response to salinity has been published contributing to an understanding of the underlying genes and regulatory mechanisms (Chen et al., 2016). The



1. Qin et al., 2013; **2.** Vadez et al., 2013; **3.** Sarkar et al., 2016; **4.** Hema et al., 2014; **5.** Patel et al., 2016; **6.** Sottosanto et al., 2007; **7.** Zhang & Blumwald, 2001; **8.** Chen et al., 2008; **9.** Xing et al., 2010; **10.** Singh et al., 2014; **11.** Sui et al., 2017; **12.** Asif et al., 2011; **13.** Bhatnagar-Mathur et al., 2009; **14.** Manjulatha et al., 2014; **15.** Pruthvi et al., 2014; **16.** Ahuja et al., 2010; **17.** Kiranmai et al., 2018; **18.** Banavath et al., 2018

Figure 2–Schematic diagram showing the list of genes and transcription factors manipulated in order to induce drought and salinity tolerance in transgenic peanut plants.

expression of Arabidopsis *AVP1* (vacuolar H^+- pyrophosphatase) gene resulted in improved salinity and drought tolerance in peanut seedlings (Qin et al., 2013). Similarly, the overexpression of *AtDREB1A* gene conferred salt tolerance in peanut through improved transpiration efficiency and growth which contributed to improved yield (Bhatnagar-Mathur et al., 2013; Sarkar et al., 2016; Vadez, Rao, Bhatnagar-Mathur, & Sharma, 2013). Apart from *AtDREB1A* gene, researchers investigated transgenic peanut plants expressing bacterial mannitol dehydrogenase (*mtlD*) gene (Hema et al., 2014; Nguyen et al., 2013; Patel et al., 2016). Another important gene that is targeted in transgenic peanut plants for inducing salt tolerance is *AtNHX1*. The Arabidopsis *AtNHX1* gene encodes a vacuolar Na^+/ H^+ antiporter to control Na^+ and K^+ vacuolar transport to modulate salt tolerance and plant development (Sottosanto, Saranga, & Blumwald, 2007). Transgenic tomato, buckwheat, tobacco, and soybean plants overexpressing *AtNHX1* from *Arabidopsis thaliana* acquired salt tolerance (Chen, Zhang, & Xu, 2008; Xing et al., 2010; Zhang & Blumwald, 2001). Similarly, transgenic peanut plants overexpressing *AtNHX1* gene showed a significant improvement in biomass under salinity thereby indicating salt tolerance (Banjara et al., 2012). Similarly, Asif et al. (2011) showed that overexpression of *AtNHX1* gene in peanut plants conferred salinity and drought tolerance. In addition to these reports, the overexpression of *SbpAPX* (peroxisomal APX) gene in transgenic peanut plants resulted in improved salinity tolerance (Singh, Mishra, & Jha, 2014). In addition, overexpression of *RabG* gene conferred salt tolerance in transgenic peanut plants and it was linked with improved photosynthetic activity, ATP synthesis through oxidative phosphorylation and downstream hormonal signaling (Sui et al., 2017).

Drought tolerance. *AtDREB1A* transgenic peanut (cv. JL24) plants exhibited considerable drought tolerance (Bhatnagar-Mathur, Devi, Vadez, & Sharma, 2009). Overexpression of a *PDH45* gene (pea DNA helicase) improved drought tolerance in peanut and hence its productivity (Manjulatha et al., 2014). The regulation of isopentenyl transferase (IPT) gene expression resulted in drought tolerance in peanut and improved its yield attributes (Qin et al., 2011b).

It is important to mention here that researchers also believe that the transfer of a single gene may not fully confer plant tolerance to multiple stresses and achieve the required level of tolerance (Bhatnagar-Mathur, Vadez, & Sharma, 2008). Rather it is more sensible to transfer a gene encoding transcription factor (TFs; Sarkar, Thankappan, Kumar, Mishra, & Dobaria, 2014). By binding specific DNA sequences, TFs offer a secondary level of control over the expression of genes under different environmental conditions including biotic and abiotic stresses to regulate growth and development accordingly (Bartels & Sunkar, 2005; Mitsuda & Ohme-Takagi, 2009; Nakashima, Ito, & Yamaguchi-Shinozaki, 2009; Yamaguchi-Shinozaki & Shinozaki, 2006). Consistent with this approach, transgenic peanut plants overexpressing *DREB1A* transcription factor showed drought tolerance and exhibited enhanced yield (Bhatnagar-Mathur et al., 2013). Similarly, constitutive over-expression of *AtDREB2A, AtHB7*, and *AtABF3TFs* genes in peanut plants resulted in higher biomass under abiotic stresses (Pruthvi, Narasimhan, & Nataraja, 2014). Thus, transgenic peanut plants encoding stress responsive genes and transcription factors can acquire improved abiotic stress tolerance. In this context, certain TF genes, for instance *DREB*, *MYB*, and *bZIP* have been identified that modulate plant molecular stress responses under various stresses (Ahuja, de Vos, Bones, & Hall, 2010). Among these, MYB TFs are the largest family of TFs and are extensively reported in eukaryotes (Du et al., 2012). So far, 30 MYB TF genes have been identified in peanut plants with their significant involvement in the biological processes (Chen et al., 2014, 2016). The involvement of MYB proteins in the regulation of plant primary and secondary metabolisms, cellular development, cell cycle regulation, hormone and flavonoid biosynthesis, and, most importantly, signal transduction and plant responses to biotic and abiotic stress conditions are reported (Dubos et al., 2008; Feller, Machemer, Braun, & Grotewold, 2011; Ma et al., 2009; Stracke, Werber, & Weisshaar, 2001). Genome-wide analysis has shown considerable diversity of TFs and their involvement in *Arachis* abiotic stress tolerance including HS (Wang et al., 2017). Recently, transgenic ground nut plants over-expressing *MuWRKY3* transcription factor conferred drought tolerance linked with better antioxidant capacity (Kiranmai et al., 2018). Similarly, transgenic peanut plants expressing an *Arabidopsis* TF (*AtHDG11*) exhibited enhanced drought and salinity tolerance (Banavath et al., 2018). Still fewer genes or TFs have been targeted to develop transgenic peanut plants for optimum yield and this approach requires further investigation.

Risks Associated with Peanut Consumption

Despite the fact that peanut has extra-ordinary medicinal, nutritional, and economic values, some of the health concerns are unfortunately linked with consumption of peanut and its derived products. These include the risk of peanut allergies and accidental exposure to fungal mycotoxins or aflatoxins. The following sections contain some details about the risks and possible management strategies for peanut consumption.

Aflatoxins

Aflatoxoins (AFs) are fungal mycotoxins or toxic secondary metabolites produced by *Aspergillus* species notably *A. flavus*, *A. parasiticus*, and *A. nomius* (Lavkor & Var, 2017; Menza, Margaret, & Lucy, 2015; Payne & Brown, 1998; Wang, Lien, & Ling, 2018) and *Emericella spp.* (Reiter, Zentek, & Razzazi, 2009). Thermodynamically, AFs are relatively stable compounds not often degraded by high temperature. The genotoxic and carcinogenic nature of AFs is one of the major health concerns (Amaike & Keller, 2011; Kensler et al., 2011; Kumar, Mahato, Kamle, Mohanta, & Kang, 2017; Wang et al., 2018). It is reported that more than 20 aflatoxins have been identified affecting crops and food derived products, and only four of them are naturally produced which pose health concerns (Boutrif, 1998; Inan, Pala, & Doymaz, 2007; Mimoune et al., 2018; Wang et al., 2018). These include aflatoxin B_1, B_2, G_1, and G_2, and they are present in peanut and its commercial products. Toxicity of AFs varies in the following order of magnitude $AFB_1 > AFG_1 > AFB_2 > AFG_2$ (Jaimez et al., 2000). In this context, AFB_1 is the most abundant mycotoxin, which is carcinogenic/mutagenic (Hamid, Tesfamariam, Zhang, & Zhang, 2013; Klich, 2007; Lai, He, Liu, & Liu, 2015; Shephard, 2018) and is classified as a group I carcinogen by WHO and the Intl. Agency for Research on Cancer (Lopez, Ramos, Bulacio, Ramadan, & Rodríguez, 2002). It is reported that AFs concentration in peanut is relatively lower than that in the peanut derived products, which may contain higher levels of AFs (Mutegi et al., 2013; Wang et al., 2018). The problem of AF contamination of food products is more commonly associated with subtropical and tropical regions (Cotty & Jaime-Garcia, 2007; Magan & Aldred, 2007; Wang et al., 2018; Zhang et al., 2017) where humidity, temperature and rainfall are important environmental causative factors (Mimoune et al., 2018; Turner et al., 2005). Peanuts like various other nuts are potentially suitable substrates for fungal pathogens, thereby can be contaminated with AFs during storage, transportation and processing, especially milling (Chen, Liao, Lin, Chiueh, & Shih, 2013; Hell et al., 2008; Martins et al., 2017; Mimoune et al., 2018; Mutegi et al., 2013).

It is pertinent to mention that prime reasons of food AF contamination include poor agricultural practices and preharvest and postharvest conditions (Lewis et al., 2005; Torres, Barros, Palacios, Chulze, & Battilani, 2014; Trucksess & Scott, 2008). Among various solutions, management practices to limit peanut AF production may include habitat management, soil amendments and improved harvesting, storage, drying, and processing practices (Lavkor & Var, 2017). In addition, the use of chemical treatments, irradiation and biological control alone or in combination is also a viable strategy (Lavkor & Var, 2017; Udomkun et al., 2017). Development of transgenic peanut plants with mycotoxin resistance has also been proposed (Jonnala et al., 2006). Recently, peanut plants with higher resveratrol content exhibited suppression in AF production by *Aspergillus* spp. (Sobolev et al., 2017). In an overall assessment, proper management of agricultural practices and the harvested crop are important aspects to minimize AF contamination (suggested readings Kumar et al., 2017; Matumba et al., 2017; Sobolev et al., 2017; Udomkun et al., 2017).

Peanut allergies

Peanut is believed to be a potent allergenic food (Valcour, Jones, Lidholm, Borres, & Hamilton, 2017) and its consumption is one of the major causes of immunoglobin E (IgE) mediated food allergies in the western populations of United Kingdom, USA, and Canada with prevalence rates ranging between 1.6% and 2.7% (Roy & Roberts, 2011; Sicherer, Muñoz-Furlong, & Sampson, 2003). It has been reported that, IgE triggers the release of histamine leading to allergic response within minutes (Johnston, Chein, & Bryce, 2014). Allergic reactions may trigger anaphylactic, fatal reactions and atopic disorders leading to life threatening conditions (Alm et al., 2009; Branum & Lukacs, 2009; Hopper, Hopp, & Durbin, 2018; Ma, Danoff, & Borish, 2014; Tomsen, 2015). Nonetheless, allergic reactions range from minor disturbances to skin, gastrointestinal tract to anaphylaxis (see extraordinary review article on food allergies by Renz et al. (2018). In this context, worldwide insights into prevalence of food allergens are documented in the literature (Tham & Leung, 2018).

The traditional way to overcome peanut allergies in children is to exclude peanut and its derived food products from the diet before the age of three (American Academy of Pediatrics, 2000). However, these practices remained ineffective and recently new recommendations suggest incorporating peanuts in the diets of infants (4 to 6 months of age) which might reduce sensitivity or allergic responses during later stages (Allen, 2017). In this context, modified U.S. guidelines for the prevention of peanut allergy 2017 have been published (Foong, Brough, Chan, & Fox, 2017) which suggest peanut early exposure to children can reduce these allergies. New evidence suggests early incorporation of peanut into the diet of infants instead of avoiding it (Suggested readings Allen, 2017; Anvari, Chokshi, Kamili, & Davis, 2016; Chen, Welch, & Laubach, 2018; Du Toit et al., 2015; Sicherer, Sampson, Eichenfield, & Rotrosenet, 2017). Above all, peanut allergies prevention guidelines have been published (Volerman & Cifu, 2016), and several ways to prevent/manage peanut allergies have also been proposed (see review articles by Allen, 2017; Chen et al., 2018).

Recommendations and Future Prospects

Peanut offers multiple benefits from plant to seed level. On the one hand, its cultivation improves soil physico-chemical properties, soil fertility being the most important, through atmospheric nitrogen fixation. On the other hand, peanuts are a rich source of medicinally important phytochemicals of diverse nature. Due to this reason peanut cultivation in developing countries can benefit local communities.

Various studies have linked peanut consumption with improved human health and with decreased risks of life threatening diseases. Apart from human health, an important task for the future will be the screening/ development of stress tolerant peanut plants. Success in this field is limited mainly due to a relatively limited focus. Apart from breeding for stress tolerance, numerous biotechnological approaches including the regulation of TFs and transfer of stress related genes can result in a significant improvement in peanut stress tolerance. Furthermore, over-expression of certain genes has induced stress tolerance in peanut. However, these biotechnological advances require further investigation especially in the context of climate change.

Moreover, a potential area of future peanut research could be the enhanced production of bioactive compounds. Numerous elicitors are reported to alter/ induce enhanced production of biologically important compounds including resveratrol, phyto-sterols, flavonoids and polyphenols, and to alter the fatty acid profile of peanut seeds. In this context, the controlled regulation of these bioactive components can benefit humans, thereby reducing the risks of heart, brain, and stomach related diseases as well as multiple types of cancer.

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