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Abstract

Peanut is an important oil, food and feed crop of the world. The kernels are rich in fats and protein, and 100 g of kernels provide 567 kcal of energy and 8.5 g of dietary fiber. Peanuts are source of minerals, vitamins and antioxidants and health improving bioactive compounds such as resveratrol, tocopherol, arginine etc. and hence are touted as functional food. Consumption of peanuts can reduce risk of inflammation, diabetes, cancer, alzheimer's and gallstone disease. Peanut is cultivated in over 100 countries, with over 95% of cultivated area in Asia and Africa. Aflatoxin and allergens are major health deterrents in peanut and more research efforts are needed to develop aflatoxin and allergen free peanuts. There is a great demand for peanut and peanut-based products in the international market, especially for confectionary types. Breeding new cultivars that meet the needs of the producers, consumers and industry is an important research area with implications along the value chain. Conventional breeding approaches and phenotyping tools were widely used to breed several varieties and in the last decade, genomic tools are integrated for making selections. The advent of next-generation sequencing (NGS) tools and the availability of the draft genome sequence of the diploid progenitors of peanut *A. duranensis* and *A. ipaensis* is expected to play a key role in sequencing the genome of cultivated peanut. Transgenic peanuts with resistance to herbicide, fungus, virus, and insects; tolerance to drought and salinity and improved grain quality are under testing at different containment levels. The availability of sophisticated tools for both genotyping and phenotyping will lead to an increase in our understanding of key genes involved and their metabolic regulatory pathways.

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2.1 Introduction

2.1.1 Name, Nomenclature, and Uses of Different Plant Parts

Peanut or groundnut is an economically important oilseed, feed, and food crop and widely cultivated in tropical and subtropical regions of the world. It is known by many local names such as earthnut, goober pea, pindas, jack nut and monkey nut. The botanical name for peanut, *Arachis hypogaea* Linn. is derived from the Greek words 'arachos' meaning a weed and *hypogaea* meaning below ground/underground chamber, referring to a weed/plant that produces fruit/pods in the soil. It belongs to the Leguminosae family, tribe *Aeschynomeneae*, and subtribe *Stylosanthenae*. It is an annual herbaceous plant, growing 30–50 cm tall and bearing tetrafoliate leaves in a 2/5 phyllotaxy (two opposite pairs; no terminal leaflet). Although peanut pods/kernels are the most important product of peanut plant, all parts of the plant are useful and can be utilized in a variety of ways.

Plant: The dried haulms after harvest constitute an energy rich fodder for cattle or in manure. A few species of peanut such as *A. glabrata* and *A. pintoii* are cultivated especially for forage purpose in South America, North America, and Australia. Another species *A. repens* is being utilized as a ground cover in South America.

Seed (kernel): The peanut seeds are consumed directly as raw, roasted, and boiled or processed into confections and peanut flour for flavor enhancement or crushed for oil for edible and industrial uses. It is also widely used in the preparation of ready to use therapeutic and supplementary foods (RUTF and RUSF) to combat malnutrition in developing countries. The peanut kernels are a source of high-quality edible oil (44–56%), easily digestible protein (22–30%), carbohydrates (10–25%), vitamins (E, K, and B complex), minerals (Ca, P, Mg, Zn and Fe) and fiber. The inferior quality oil has a variety of industrial uses. Paint, varnish, lubricants, leather dressings, furniture polish, insecticides, nitroglycerine, soap, and cosmetics are all prepared from the oil. The protein portion of the oil is

utilized in the manufacture of some textile fibers (Bell 2008).

Peanut skin: Peanut skins are obtained from processed nuts, broken nuts and sometimes from nuts not found fit for human consumption. They are a good source of several bioactive compounds mainly phenolics and have long been used in China as a traditional Chinese medicine for the treatment of chronic hemorrhage and bronchitis. They are also added as supplements to processed food products such as peanut paste and peanut butter to improve flavor, stability and antioxidant capacity (Hathorn and Sanders 2012).

Peanut cake: This byproduct of oil extraction is used in animal feed industry, in making weaning foods for children, invalid foods for aged people and as fertilizer.

Shell: The shells are used as fuel, animal feed, cattle litter, filler in feed and fertilizer industry and in making particle boards, and alcohol and acetone after fermentation. They are also used to make cellulose (used in rayon and paper) and mucilage (glue) (Bell 2008).

Roots: Being a legume crop the roots add nitrogen (100–152 kg/ha N) and organic matter to the soil (Nigam 2015).

2.1.2 Area, Production, and Growing Regions

Peanut is cultivated in 25.70 million ha world over with a total production of 42.32 million tons of in-shell peanuts during 2014 (FAOSTAT 2015). China (22%), India (19%), Nigeria (11%), and the USA (2%) are the major peanut growing countries. China (42%) and India (18%) account for about 60% of the total production globally followed by Nigeria (7.7%), the USA (4.3%) and Indonesia (1.8%) (Rathnakumar et al. 2013). Africa with 12.40 m ha area and 11.54 m tons of production, and Asia with 11.87 m ha and 29.95 m tons, together account for 95% global peanut area and 91% of global peanut production. Since 1980, the global peanut production increased by 2.67% annually until 2014 and this increase was contributed by an increase in both

cultivated area (0.93%) and yield (1.74%) (FAOSTAT 2015). In Asia, the annual growth rate in terms of area cultivated and production increased by 0.05% and 2.60% during the same period while that of Africa was much higher with 2.46% and 3.62% increase in area and production. In terms of peanut oil production, China with 2.74 m tons in 2015/16 was the top producer followed by India (1.1 m tons) and Myanmar (0.27 m tons). India's share in global production of peanut oil is expected to be around 20% in 2015–2016.¹

Peanut is cultivated in more than 100 countries across the world under different agroecological environments. However, the major cultivation is confined to the developing countries of Asia and Africa which accounts for a bulk of the total peanut area as well as production. The share of Asia in global peanut area and production in 1990 was 65.70 and 70.52% respectively while in 2014 it was 43.62 and 59.79% respectively, indicating a declining trend (Fig. 2.1). In comparison, the African share increased from 27.68 and 19.31% in 1990 to 51.01 and 29.79% respectively in 2014 (Fig. 2.2). China in East Asia, India in South Asia and Myanmar, Indonesia, Vietnam, and Thailand in Southeast Asia are the major Asian peanut producing regions.

2.1.3 Yield and Production Constraints

Peanut yields increased worldwide by 1.74% per annum between 1980 and 2014. In 2014 the world average productivity of in-shell peanuts was 1648 kg/ha which was lower as compared to 1823 kg/ha in 2013. Cyprus, Israel, Barbados, Nicaragua, and USA were the top 5 highest yielders during 2013–2014 (FAOSTAT 2015). In the Asian context, China was the top yielder in 2014 with an annual yield of 3490 kg/ha, as compared to 1261 kg/ha of India. During the period of 1980–2014, China showed 4.71%

positive annual growth rate while it was 1.40% for India (FAOSTAT 2015). Vietnam (145%), Indonesia (33%), Thailand (32%) and Myanmar (81%) in Southeast Asia experienced spectacular increase in yield during 1981–1983 to 2012–2014 and most of this increase was contributed by the introduction of high-yielding, stress-resistant varieties and improved production practices such as balanced fertilization, efficient weed and chemical pest control, use of polythene mulches and improved technology dispersal systems. The yield increase in China and India during the same period was 116 and 53%, respectively. As compared to regional variation, considerable yield difference is also observed between developed and developing countries which are mainly due to the different production systems being practiced. Peanut is grown in two distinct production systems—low-input system practiced by the farmers of Africa and South Asia and the high-input production systems. In the low-input system, farmers cultivate low-yielding, late-maturing varieties on marginal lands with no irrigation and limited inputs with average yields ranging from 800 to 1000 kg/ha. In high-input production systems practiced in the USA, Australia, Argentina, Brazil, China and South Africa, peanut yields can vary from 2 to 4 t/ha. Here cultivation of peanut is commercialized using improved varieties, modern crop management practices, irrigation and high resource inputs along with fully mechanized farming.

Productivity levels of peanut in most of the developing countries have remained low due to several production constraints which include biotic and abiotic stresses, lack of efficient seed dispersal systems, technological knowhow, market accessibility, low-input use and factors related to socio-economic infrastructure. Insect pests, diseases, drought, and low soil fertility are the major biotic and abiotic stresses. Most of the peanut cultivation in the developing countries is carried out by smallholder farmers who lack adequate resources or access to novel technologies to improve productivity. Additionally, limited market access and low producer prices reduce the incentive for producers to invest in productivity-enhancing technologies such as

¹http://www.agricoop.nic.in/Admin_Agricoop/Uploaded_File/edib_2201.pdf.

Fig. 2.1 Yearly average variation for area, production and yield of peanut in Asia during the period from 1990 to 2014

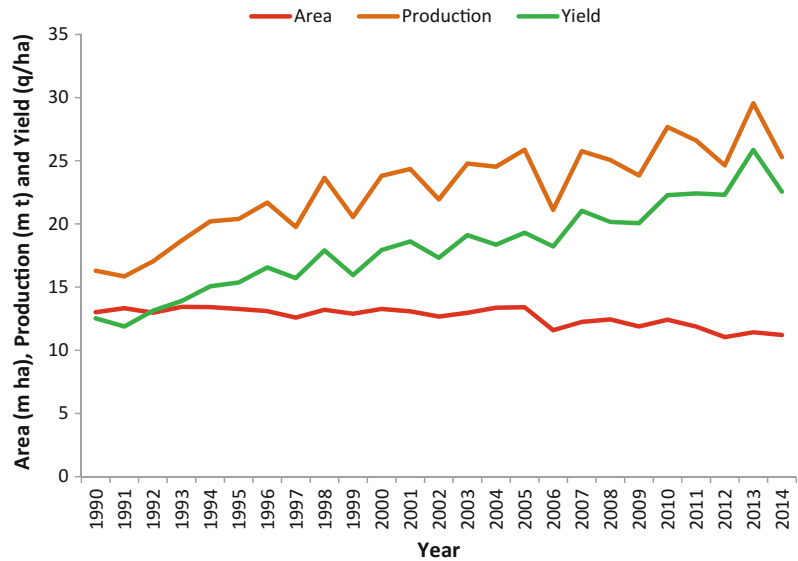
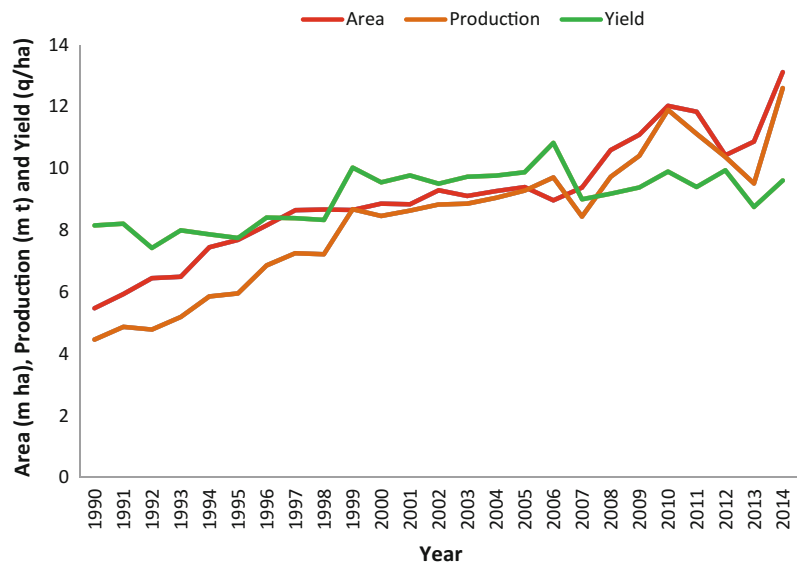


Fig. 2.2 Yearly average variation for area, production and yield of peanut in Africa during the period from 1990 to 2014



improved seed, fertilizers, and pesticides resulting in low yields. One major constraint is the lack of improved varieties suited to different agroecological zones and availability of effective seed dispersal systems. Due to non-availability of seeds or efficient dissemination on information of new varieties, the majority of smallholder farmers still grow traditional landraces/outdated varieties that are adapted to local environments but have low genetic yield potentials and are, in

many cases, susceptible to drought, pests, and diseases. Lack of efficient storage structures and low storability of peanut seeds under ambient conditions is another important constraint. Seed being a costly resource, many smallholder farmers tend to retain seeds from previous harvests for use in subsequent season. However, poor storage conditions and low use of seed-treatment chemicals further reduce the quality of the seed. The private seed sector

companies are hesitant to invest in peanut seed multiplication and distribution because the crop has high seed requirement, low multiplication factor, the bulky nature of the seed and low storability under normal conditions. Aflatoxin contamination of peanut by the fungi *Aspergillus flavus* and *A. parasiticus* is an important constraint affecting the quality of peanut in most producing countries in Africa and Asia. Aflatoxin contaminated peanuts are potent carcinogens for both humans and livestock and many importing countries have placed strict restrictions on acceptable levels of aflatoxin in peanut. Besides, the policy regulations restricting movement of seeds and marketable peanut products have hampered the development of the peanut sector, in many producing countries and especially in Africa.

2.1.4 Trading of Peanut

There is a great demand for peanut and peanut-based products in the International market, especially for confectionary types. In 2010–2013 an estimated 42 MMT (million metric tons) of peanuts were utilized annually in the world which was an increase of approximately 134% from 18 MMT in the 1970s (Fletcher and Shi 2014). Export or import to any country is guided by regulations and requires strict adherence to consistency in supply and in quality of the produce. Increasing the exports quantity is the primary objective as it earns foreign exchange for the country and also benefits the supply chain comprising of producers, processors, and traders. International trade of peanut is primarily in the form of pods (in-shell), shelled (kernels), meal (cake) and as oil. Over the past decades trade volumes have increased substantially for confectionary peanut but fallen for peanut oil and meal due to availability of cheaper substitutes such as soybean and raising concerns over aflatoxin contamination. Besides the higher nutritional quality of peanuts for food purpose, development of novel peanut-based food products and initiatives by the American Peanut Council for export promotion and education has

led to improvements in existing peanut markets and developing new peanut-based markets for food use. In 2010–2013, about 41% of the world annual peanut production was crushed for domestic use, 45% for domestic food use and the remaining 14% was exported, used for feed or lost. Food use of peanut has increased by about 265% and crushing use increased by about 75% since the 1970s (Fletcher and Shi 2014).

2.1.4.1 Peanut Oil

International trade of edible oil has declined over time as the major producers of the crop *viz.* China, India, and USA consume substantial amounts of edible oil in their domestic markets leaving very little surplus for export. The export trade of oil in the developing countries is concentrated mainly in Senegal and Sudan accounting for one-third of global exports. Among the developed countries, USA with 13% of world exports is the only significant exporter of peanut oil (Freeman et al. 1999). In 2008–2009, the USA, Argentina, Sudan, Senegal, and Brazil took about 71% share of the global export and the European Union (EU), Canada and Japan 78% share of global import in international trade of peanut (Rathnakumar et al. 2015).

2.1.4.2 Peanut Kernels

Trading of shelled peanut has increased in recent times. Developing countries accounted for much of this increase. However, the utilization pattern varied across the regions. Fast-growing Asian economies such as China are devoting more peanuts to consumption due to rising per capita incomes and urbanization. During 2013, the global import of shelled peanut was 1.68 m tons estimated at US\$ 2467 million while the global export stood at 1.67 m tons estimated at US\$ 2195 million. India (388 k tons), Argentina (190 k tons), USA (177 k tons) and China [China (176 k tons), China mainland (176 k tons)] were the top five exporters of shelled peanuts during 2005–2013 while EU (448–497 k tons) was the top importer of shelled peanut followed by Netherlands (288 k tons) in the same period (FAOSTAT 2015).

2.1.4.3 Peanut Meal

Peanut meal is an important source of protein for livestock. The production and trade of peanut meal is directly influenced by demands for peanut oil, competing prices between other oilseed meals and cereal-based-substitutes and the existing tariff barriers. During the period, 1979–1981 to 1994–1996, world utilization of peanut meal increased by 45% with most of the increase coming from Asia. The demand was more pronounced in Thailand, Indonesia, and some other rapidly developing Asian countries due to increased consumption of meat and livestock rearing. In the developed countries consumption declined by 60% during the same period, because of developments in the European market, which show the share of European Community in global utilization of peanut meal fall from 22% in 1979–1981 to 5% in 1994–1996. This decline was mainly due to increase in peanut meal prices, presence of aflatoxins in imported products beyond the permissible limit and its subsequent substitution by cheaper feed alternatives such as soybean meal.

The trading of peanuts in the International market requires strict adherence to aflatoxin content levels and is recognized as the primary non-tariff trade barrier for export of peanut by the developing countries such as Asia and Africa. The magnitude of losses incurred due to trading of aflatoxin contaminated peanuts is not known, but they have serious economic implications in terms of visible and invisible costs both at national and international level. The permissible limit varies among the countries—35 ppb (total) by Malaysia; 30 (ppb) total by India, Indonesia and Brazil; 20 ppb (total) by the USA, Kenya, and the Philippines; 15 ppb (total) by Canada, UAE and Australia; 10 ppb (B₁) by Japan, Korea, Taiwan and Singapore; 10 ppb (total) by Egypt and Vietnam; 5 ppb (B₁) by the Russian Federation and Turkey. However, the EU countries have set a very stringent maximum permissible limit of 2 ppb for B₁ and 4 ppb for total aflatoxins in peanuts. This new trade regulations led to decline in imports of peanut meal to EU countries from 0.91 Mt in 1979–1980 to 0.43 Mt

in 1989–1990 (Bhat 1991). Similarly, the export of peanut meal from India declined from 550 t valued at US\$ 42.5 million in 1977–1978 to 265 t valued at US\$ 32.5 million in 1985–1986, mainly because of aflatoxins (Bhat and Rao 1990).

2.2 Nutritional Value

2.2.1 Kernels, Meals and Haulms

Peanut seeds (kernels), the most important product of peanut are a rich source of nutrition and provide several health benefits. The kernels contain 40–55% oil, 20–35% protein and 10–20% carbohydrate. They provide 567 kcal of energy from 100 g of kernels (Jambunathan 1991). The peanut oil contains seven fatty acids of which palmitic (7–12%), oleic (40–50%) and linoleic (25–35%) together account for approximately 90% of total fatty acids. High oleic lines containing >80% oleic acid are also available. Also, the seeds are good source of minerals like calcium, phosphorus, iron, and zinc; vitamins like E, and the B-complex groups of thiamin, pantothenic acid, riboflavin, foliates and niacin; antioxidants like *p*-coumaric acid and resveratrol; and biologically active polyphenols, flavonoids and isoflavones. Peanut meal obtained after oil extraction is a high protein rich feed for livestock and poultry. The primary constituents are crude protein (45.6%), sugar (32.50%), fat (2.5%), fiber (8.3%) and ash (5.0%). It is also a rich source of amino acids- lysine, methionine, cysteine, threonine and arginine, and minerals such as calcium, phosphorus, sodium, and potassium. The metabolizable energy of peanut meal is 2664 kcal/kg (Batal et al. 2005). Peanut haulms (the above ground vegetative part) is a good source of nutritious fodder for livestock, and contains protein (8–15%), lipids (1–3%), minerals (9–17%), crude fiber (22–38%) and carbohydrates (38–45%). It is used as cattle feed in fresh or dried stage, or by preparing hay or silage. Nutrient digestibility in the case of peanut haulms is around 53% and that of crude protein

is 88% when fed to animals (Nagaraj 1988). Haulms are capable of releasing energy up to 2.337 cal/kg of dry matter.

2.2.2 Food Products

Several value-added products developed from peanut are available around the world such as peanut flour, roasted and boiled peanut (in-shell/kernel), peanut butter, peanut candy etc. Local delicacies have also been developed for localized consumption purpose. For example, in many parts of Western Africa and Sudan partially defatted or full-fat peanut is a local delicacy and the most common form of utilization. Partially defatted peanut paste is produced after the oil has been extracted, and is used for making *kuli-kuli* in Nigeria and *coura-coura* in Burkina Faso. The full-fat peanut paste is a common food ingredient in Western Africa, Sudan and Southern Africa (Freeman et al. 1999).

2.2.3 Consumption Pattern

There is a visible divergence in the consumption pattern of peanut both in the developed and developing countries. Most of the peanut produced in the developing countries is crushed for extraction of oil to meet the domestic consumption needs, while in the developed countries such as USA it is mainly consumed as a food source. Over the years, even in developing countries, the trend has shifted more towards food source with increasing international market demands for confectionary grade peanuts and the availability of other cheaper alternative oils. In Africa, peanuts are consumed as roasted, boiled or raw and as peanut paste. In Argentina and Brazil, large quantities of confectionary peanut are consumed as roasted nuts or in packaged form as snack foods such as peanut candy. In USA, peanut consumption is mainly in the form of peanut butter, packaged snack nuts (salted, unsalted, flavored and honey-roasted) and peanut candies.

Even among countries, diversity exists in terms of regional preferences. For example, the

food consumption of peanut dominates in North America and the oil consumption dominates in the South. In East and West Africa, both food and oil uses dominate while in South Africa the food use of peanut is dominant. In Southeast Asia, the food use dominates while in Southwest Asia, which is dominated by India, oil use is more important over food use (Rathnakumar et al. 2015).

2.2.4 RUTF and Food Supplements

Malnutrition is one of the most serious issues threatening the global community and especially in the developing countries. Globally it is estimated that about 20 million children suffer from severe acute malnutrition (SAM) of which about 8.1 million children are from India. One way of combating malnutrition issues is to provide the affected individuals with essential nutrients, minerals and vitamins in an easily available and ready to use form. Therapeutic foods are nutritionally enhanced food products, supplied in emergency situations for the treatment of SAM symptoms. Peanut is one of the important constituent of such product due to its balanced nutrient composition. Ready to use therapeutic food or RUTF originally referred to a nutrient dense and energy-dense peanut-based paste designed specifically for the treatment of SAM in young children. There are different types of RUTF currently available in the market, among which the 'Plumpy nut' patented product by Nutriset is widely recommended by UNICEF. This nutritional paste (peanuts, powdered milk, vegetable oil, sugar, vitamin and mineral mix) contains the right mix of nutrients to treat a child with SAM, and in a form that is easy to consume and safe. RUTFs provide 520–550 kcal/100 g (Kapil 2009; Dubey and Bhattacharya 2011).

Another product line Ready to use Supplementary Food (RUSF) is produced and marketed by Nutriset. RUSFs are foods that are fortified with micronutrients as a remedy for malnutrition and can be consumed without cooking or the addition of water. This product aims to tackle malnutrition at early stages (moderate acute

malnutrition, or in prevention of acute malnutrition or chronic malnutrition) and are used in addition to breastfeeding (for young children above 6 months of age) and traditional complementary food. The RUSF product line includes Plumpy doz, Supplementary Plumpy, QBMIX, and Delphia infant milk (Latham et al. 2011).

2.2.5 Functional Food Use of Peanuts

Peanuts are a good source of wide range of nutrients and bioactive compounds with health benefits. Most of these compounds are either present in the skin, the extracted oils and the kernels. Even the methanolic extracts from peanut hulls were reported to have strong antioxidant activity (Duh and Yen 1995) and ability of scavenging free radical and reactive oxygen species (Yen and Duh 1994). They are touted as functional foods due to the presence of numerous functional components like Coenzyme Q10. These bioactive components are widely recognized for their disease preventative properties. Some of the bioactive compounds such as tocopherols, tocotrienols, flavonoids and resveratrol function as antioxidants while others promote longevity.

2.2.5.1 Tocopherols

Tocopherols (TCP) are a class of organic chemical compounds having vitamin E activity. Peanut oils are a good source of α and γ -tocopherols with contents varying from 50–373 ppm and 90–390 ppm respectively (Firestone 1999). The diversity depends on the origin (Sanders et al. 1992), variety, maturity and the growing conditions. Higher tocopherol content was consistently reported from US developed peanuts as compared to those produced in China or Argentina. Under same growing conditions runner varieties have higher levels of α -, γ - and δ -tocopherols than the Spanish varieties.

2.2.5.2 Resveratrol

Resveratrol (3, 5, 4'-trihydroxystilbene) is a naturally occurring stilbene phytoalexin polyphenol. It is naturally produced by several

plants in response to injury, stress, infection, or ultraviolet (UV) radiation (Jeandet et al. 2012). Resveratrol is reported to play positive roles in reducing cancer risks, heart diseases, tumor and inflammation (Arya et al. 2016). Peanuts are excellent sources of resveratrol with the southern style boiled peanuts having the most abundant, even more than that found in red wine and red grape juice on a part per million basis (Sanders et al. 2000) followed by peanut butter (Ibern-Gomez et al. 2000). All parts of the peanut contain resveratrol from the roots to the skins and even the shell (Francisco and Resurreccion 2008).

2.2.5.3 Phytosterols

Phytosterols or plant sterols, a naturally occurring compound found in plant cell membranes are minor components of all vegetable oils and constitute major portion of the unsaponifiable fraction of the oil. Peanut oil contains 900–3000 ppm total phytosterols of which β -sitosterol (>80%), campesterol (10%) and stigmasterol (<5%) together constitute 95% (Firestone 1999). Phytosterols due to their structural similarity with cholesterol block the absorption of cholesterol in the digestive system thereby reducing the risk of cardiovascular diseases. People who consume small amounts of peanut daily were found to have lesser instance of heart-related diseases (Awad et al. 2000). Emerging evidence has shown that they also reduce inflammation and reduce the growth of various cancers (Woyengo et al. 2009).

2.2.5.4 Arginine

Arginine is an amino acid that plays an important role in strengthening the body's immune system, regulating hormone and blood sugar levels and promoting male fertility. It is considered semi-essential because, although the body can manufacture its own supply, dietary supplementation may become essential under certain situations of severe injury and illness. Peanuts have the highest level of arginine among foods (USDA SR-21). Arginine is the precursor to nitric oxide which helps to keep the arteries relaxed, improve

the blood flow and healing time in tissues in the body (Moncada and Higgs 1993).

2.2.5.5 Phenolic Acids and Flavonoids

Peanut and peanut skins are a good source of phenolic compounds (Francisco and Resurreccion 2008) especially p-coumaric acid. Peanut skins are often added to processed foods such as peanut paste and peanut butter to improve shelf-life, antioxidant capacity, and nutritional quality. Phenolic acids have been shown to play a protective role against oxidative damage diseases like coronary heart disease, stroke, and various cancers. It was further reported that roasted peanuts have phenolic acid levels comparable to those found in green tea and red wine, and more than those in berries when the skin is not removed (Francisco and Resurreccion 2008).

Flavonoids are a group of secondary biochemicals that mostly function in plant defense systems. They act as natural pesticide, some provide potent odors or bitter flavors as a defense system, while others are antimicrobial in nature. They are present throughout the peanut plant and are responsible for color, taste, and protection of vitamins, enzymes and fat oxidation. A high intake of flavonoids reduces chances of heart-related diseases and various types of cancer by diverse mechanisms which are still being researched.

2.3 Taxonomic Classification

2.3.1 Plant and Floral Biology

The cultivated peanut is an allotetraploid ($2n = 4x = 40$) and is believed to have originated from a cross involving the diploid species *A. duranensis* and *A. ipaensis* (Kochert et al. 1996; Seijo 2004, 2007). The main stem of the plant is either upright or prostrate (12–65 cm in length) and develops from a terminal bud of the epicotyl, while two cotyledonary laterals (prostrate, runner type or upright) grow on opposite sides. The stem usually bears tetrafoliate leaves, with leaflets on the main stem differing in shape and size from those on lateral branches.

Peanut flowers are typically papilionaceous and zygomorphic and represented either by a solitary flower (simple inflorescence) or by a raceme containing two to five flowers (compound inflorescence) in the axils of the cataphylls. The flowers are borne aerially but pod development takes place below the ground due to geotropic movement of the gynophores (pegs). Flowering in peanut is sensitive to light, temperature and relative humidity. Temperatures between 22 and 33 °C and soil moisture of 40% are ideal for flowering, while light intensity >45% of full sunlight helps in optimum floral development. Under normal conditions, flowers open at sunrise, but low temperature can delay the opening. Anther dehiscence can take place 7–8 h before flower opens in some varieties whereas in others they may not do so even at flower opening (Bolhuis et al. 1965). The stigma becomes receptive about 24 h prior to anthesis and its receptivity can persist for about 12 h after anthesis. Self-pollination takes place within the closed keel of the flower. About 40% of the flowers fail to begin pod development and another 40% abort before pod development.

2.3.2 Center of Origin and Distribution

The exact center of origin of peanut is unclear but it is believed to be somewhere in the region of eastern foothills of the Andes (southern Bolivia to northwestern Argentina) because of the primitive characters (pod beak, pod shape, pod reticulation etc.) associated with germplasms from the region (Krapovikas 1969; Gregory et al. 1980). It is naturally restricted to Argentina, Bolivia, Brazil, Paraguay, and Uruguay in South America. The greatest genetic diversity in *Arachis* was reported in South America with six recognized gene centers for cultivated peanut in South America—(i) the Guaraní region, (ii) Goiás and Minas Gerais (Brazil), (iii) Rondonia and northwest Mato Grosso (Brazil), (iv) the eastern foothills of the Andes in Bolivia, (v) Peru, and (vi) Northeastern Brazil. A seventh center Ecuador was added to the group following

identification of distinct group of landraces referred as var. *aequatoriana* (Krapovickas and Gregory 1994, 2007).

The domestication of peanut probably happened in the valleys of the Parana and the Paraguay river systems in the Gran Chaco area of South America (Hammons 1994). Remnant single-seeded peanut shells recovered from archeological excavations in coastal Peru dating back to 800 BC evidenced the cultivation of peanut. From South America, the peanut spread to other parts of the world. The ‘Virginia variety’ was taken from the Antilles to Mexico around 1500 and then quickly introduced into West Africa. Subsequently, it was introduced into North America in the 17th century. Portuguese explorers in the late 15th century carried 2-seeded ‘Spanish’ peanut varieties from South America (Brazil) to Africa, where it got mixed with the ‘Virginia’ types and produced a great diversity of African land races. The Spaniards in the early 16th century took 3-seeded Peruvian types (including *hirsuta* types) to Philippines and then to southeastern China where it was referred to as ‘foreign beans’ (Nigam 2015). From there it spread throughout China and to Japan as ‘Chinese beans’. The ‘Valencia types’ were taken from Cordoba, Argentina around 1900 and introduced into Spain and subsequently to USA from Valencia during 1910 (Rathnakumar et al. 2013).

2.3.3 Classification

The genus *Arachis* based on morphology, geographical distribution and cross compatibility has been divided into nine taxonomic sections and comprises of 80 described species (Krapovickas and Gregory 1994, 2007; Valls and Simpson 2005), which includes both diploids and tetraploids belonging to either annual or perennial type. Among them *Arachis hypogaea* L. is the only cultivated species. It is a tetraploid (amphidiploid or allotetraploid) with a chromosome number $2n = 4x = 40$. Besides, *A. hypogaea*, two other species *A. villosulicarpa* (cultivated in

northwestern Brazil) and *A. stenosperma* (cultivated in central and southwestern Brazil) are grown for their seeds.

The cultivated peanut is divided into two subspecies, sub sp. ‘*hypogaea*’ and subsp. ‘*fastigiata*’ based on the branching pattern and the distribution of vegetative and reproductive axes. The former subspecies is characterized by the absence of reproductive axes (flowers) on the main stem and the presence of alternate pairs of vegetative and reproductive axes on the cotyledonary laterals and $n + 1$ lateral branches (called alternate branching pattern). The latter is characterized by the presence of reproductive axes on the main stem and the presence of reproductive axes on successive nodes of lateral branches (called sequential branching). The subsp *fastigiata* is comprised of four botanical varieties, var. *fastigiata*, var. *vulgaris*, var. *peruviana*, and var. *aequatoriana*, while subsp *hypogaea* is divided into two varieties, var. *hypogaea* and var. *hirsuta* based on inflorescence, pod and seed characters.

2.3.4 Market Types

Based on popularity and market uses four types of peanut has been defined in the United States: Spanish, Runner, Virginia, and Valencia. The large-seeded Virginia types are the most widely cultivated peanut in the Virginia-North Carolina area; the runner market type is grown predominantly in the Southeast and Southwest America, and the Spanish types are grown in Texas and Oklahoma. The Valencia market types are mostly produced in New Mexico for the in-shell market (Holbrook and Stalker 2003). Depending on differences in flavor, oil content and quality, size and shape of pods and kernels certain types are preferred over others; but for most cases the different types are interchangeable. In the US most peanuts marketed in the shell are of the Virginia type, along with some Valencia selected for large size and attractive appearance of the shell. Valencia peanuts are very sweet in taste and are also excellent for consumption as boiled peanuts. The Spanish types are mostly used for

making peanut candy, salted nuts, and peanut butter. The runner types are mostly preferred for making peanut butter.

2.4 Peanut Research

2.4.1 Breeding New Varieties

Hybridization between selected parents, selection using phenotyping and advancing the generations, followed by yield trials have led to development and release of several varieties suitable to varying production environments and meet the needs of the producers, consumers, and industry (Janila and Nigam 2013). Among the different traits, breeding for high yield is the most important yield component for determining performance of new varieties, although kernel yield and oil yield are considered under special circumstances such as for developing high oil lines. In India 194 peanut varieties have been released by 2012 which have contributed to increased yield. However, most of the yield improvements came through increase in number of pods and improvements in pod and seed size (Reddy 1988; Ratnakumar et al. 2010, 2013). Varieties such as Vijetha, Girnar-3, GPBD-5, ICGV 00350, RARS-T-1, GJG-31, GJG-9 were released following their superior yield performance in national trials (Ratnakumar et al. 2013). Starting from 1976, ICRISAT has developed and released 179 peanut varieties across 38 countries globally. In China, yields of 9 t/ha were obtained from improved cultivars when grown under favorable conditions (Yu 2011). Along with yield, the length of the growing period (LGP) and resistance to pathogens and pests are important to enable adaptation of peanut to new regions or special cropping systems.

Among the fungal diseases, early leaf spot (causal agent *Cercospora arachidicola*), late leaf spot (*Phaeoisariopsis personata*) and rust (*Puccinia arachidis* Spegazzini) are important foliar

pathogens and are the focus of most peanut breeders across the world. Varieties with resistance to foliar fungal diseases were reported (Singh et al. 1997). Very high levels of resistance to foliar fungal diseases occurs in related wild species of peanut but has limited utility as a consequence of undesirable genetic linkage between resistance and low yield, late maturity, low shelling outturn, heavy pod reticulation, bitter kernels etc. (Liao 2014). Bacterial wilt (BW) caused by *Ralstonia solanacearum* is a major production constraint of peanut in China, Indonesia, Vietnam, and Uganda. Breeding efforts for BW resistance concentrated on screening and identifying BW resistant lines (Singh et al. 1997; Hong et al. 1999). Among the viruses groundnut rosette disease (GRD) in Africa, peanut bud necrosis disease (PBND) in India, tomato spotted wilt virus (TSWV) in East and South east Asia, peanut stem necrosis disease (PSND) in some areas in southern India, and peanut clump virus disease (PCVD) in West Africa are major breeding targets worldwide. Breeding for virus resistance has achieved significant progress with the identification of resistant and tolerant lines both among cultivated and wild *Arachis* sp. (Upadhyaya et al. 2011; Nigam 2015).

Both, physiological trait-based and empirical selection approaches are used for improving drought tolerance in peanut. Breeding heat tolerant genotypes has become a priority with changing climatic conditions and increase in temperature. Nutritional quality aspect of peanut is gaining importance worldwide with the development of high-end tools for quality assessment and their requirement in different products. For example, in confectionary peanut, the quality attributes targeted include high sugar, high protein, low oil, attractive seed size and shape, pink or tan seed color, ease of blanching and high oleic/linoleic ratio, while for developing RUTF and food supplement based products, peanuts with high protein, minerals and vitamins

are preferred. For edible oil and biofuel purpose, varieties with high oil content and specific fatty acid profiles are desired.

2.4.2 Genetics of Important Agronomic Traits

A thorough knowledge of nature of inheritance, interaction with the environment, the nature of gene action and the number of alleles/genes involved in governing agronomically important traits is key to target their improvement. Most agronomic traits in peanut are inherited quantitatively and are highly influenced by genotype \times environment interactions. The genetics of several important target traits in peanut have been studied and this information is well documented (Reddy and Murthy 1996; Nigam 2015). In peanut, pod yield is the most important and complex trait and it is associated with over 40 other traits (Murthy and Reddy 1993). Genetic studies have identified both additive and non-additive components of genetic variances to be important for yield and related traits. Significant cytoplasmic influence on yield and related characters was also observed (Dwivedi et al. 1989). Oil content in peanut is controlled by both additive and non-additive components of gene action. The low levels of genetic variability were a major hindrance in breeding for high oil content in peanut seeds. Identification of high oil lines both among cultivated and wild *Arachis* species has accelerated breeding efforts to develop cultivars with oil content higher than 55%. Iodine value, an indicator of oil quality and stability has been reported to be governed predominantly by additive gene action (Basu et al. 1988). The high oleic trait in peanut is controlled by two recessive genes located on the A and B genomes (Knauff et al. 1993).

Genetic studies for drought tolerance are mainly restricted to its contributing surrogate traits as it is very difficult to measure it under

field conditions. Sufficient variability for physiological traits such as specific leaf area (SLA), soil water extraction ability, water use efficiency and harvest index (HI) was observed among tolerant and susceptible genotypes. It was reported that both additive and additive \times additive gene effects for SLA and HI and additive gene effects for $\Delta^{13}\text{C}$ (carbon isotope discrimination) are the major genetic factors (Nigam et al. 2001).

Studies on genetics for rust resistance in cultivated peanut has revealed that it is governed by two or more recessive genes interacting in various ways (Nigam 2015). However, the resistance in wild *Arachis* species is controlled by dominant genes (Singh et al. 1984). Resistance to early and late leaf spot has been reported to be independently controlled by two or more major genes (Tiwari et al. 1984) and several minor genes predominantly with additive effects (Anderson et al. 1986). In the wild species, resistance to ELS and LLS was reported to be independently inherited (Nigam 2015). Aflatoxin contamination is a major problem in large and extra-large kernelled peanut genotypes and those exposed to drought stress. Three levels of resistance mechanism were identified—preharvest resistance, seed coat resistance (in vitro seed colonization) and cotyledon resistance (aflatoxin production). For *A. flavus* infection a pair of major genes with additive value of 0.38 and a pair of minor genes with additive value of 0.12 was reported in literature (Zhou et al. 1999; Zhou and Liang 2002). Seed coat resistance has been reported to be controlled by predominant additive genes and maternal genotype (Rao et al. 1989). Resistance to PBNB has been reported to be governed by three factors (Pensuk et al. 2004). For TSWV significant general combining ability (GCA), specific combining ability (SCA) and transgressive segregation was reported but the genetic mechanism of resistance is yet to be elucidated. In the case of GRD (effective against GRV and its SatRNA) resistance in cultivated types is

reported to be governed by two independent recessive genes which are effective against both chlorotic and green rosette (Olorunju et al. 1992).

2.4.3 Genomic Tools and Genome Sequence

Use of genomics based approaches for improvement of economically important target traits in peanut has been challenging due to its inherent genetic architecture. Narrow genetic base of the primary gene pool, tetraploid nature of the cultivated peanut and cultivation of limited genotypes in the process of domestication has resulted in diminishing genetic resources and low variability for several traits. Presence of quantifiable variability is a must to identify linked molecular markers and/or quantitative trait loci (QTLs) for marker-assisted breeding for crop improvement. Among all genomic tools, molecular markers have proved to be the most useful in characterizing and harnessing available genetic variations. The early generation markers were basically used for conducting genetic diversity studies (Bravo et al. 2006), in limited cases for construction of genetic maps (Garcia et al. 2005; Leal-Bertioli et al. 2009) and identification of associated genes/QTLs (Herselman et al. 2004). The development of more efficient marker systems such as Simple Sequence Repeat (SSR), Single Nucleotide Polymorphism (SNP) etc. led to identification of closely linked markers for several target traits such as resistance to nematode, ELS and LLS, rust, high oleic acid, drought tolerance and their utilization in breeding programs worldwide (Pandey et al. 2014). The different marker systems in peanut and their utilization in trait breeding is reviewed in Janila et al. (2016).

Although genetic mapping studies of peanut started in the late 20th century (Halward et al. 1993), the first report of genetic map of cultivated peanut was published in 2009 (Varshney et al. 2009). Since then, efforts have been directed towards refining the genetic map using mapping populations (Khedikar et al. 2010) or through construction of composite linkage maps (Hong et al. 2010) and integrated maps (Qin et al.

2012). The first international reference consensus map for tetraploid peanut was constructed by Gautami et al. (2012) based on data obtained from 11 populations. The map had 897 marker loci (895 SSR loci and two cleaved amplified polymorphic sequences (CAPS)) distributed on 20 linkage groups and spanning a map distance of 3863.6 cM with an average map density of 4.4 cM. Considering the huge potential offered by SNPs in marker trait association studies, efforts were also made to develop SNP based linkage maps in peanut. The first SNP marker based genetic map was developed for the AA genome of peanut (Nagy et al. 2012). This was followed by the development of an SNP based linkage map for the cultivated peanut. The linkage map was constructed using 1685 marker loci (1621 SNPs and 64 SSRs) spanning a distance of 1446.7 cM (Zhou et al. 2014).

With the advent of Next-Generation Sequencing (NGS) technology platforms, sequencing the peanut genome has now become a distinct possibility. NGS technologies offer faster sequence data generation and informatics tools to manage and analyze NGS data (Varshney and May 2012) in a relatively short time. To sequence the peanut genome, the Peanut Genome Consortium (PGC) was formed for the tetraploid cultivar “Tifrunner”.² Very recently, the genome sequences of *A. duranensis* and *A. ipaensis*, the diploid ancestors of cultivated peanut was completed (Bertioli et al. 2016). The sequence information will be useful to identify candidate disease resistance genes, to develop molecular markers, to guide tetraploid transcript assemblies and to detect genetic exchange between cultivated peanut’s subgenomes.

2.4.4 Aflatoxin and Allergens

Two quality deterrents- aflatoxin contamination and allergens play a significant role in determining the industry and consumer base and the marketability of the produce. Contamination of

²<http://www.peanutbioscience.com/peanutgenomeproject.html>.

peanuts by aflatoxin is a global issue forcing many countries to have strict restrictions with regards to aflatoxin content in the produce. Aflatoxins are secondary metabolites produced by colonization of peanut kernels by *Aspergillus flavus* (Link) and *Aspergillus parasiticus* (Spear) and are considered among the most potent carcinogenic mycotoxins in nature. Peanuts are susceptible to *Aspergillus* infection and aflatoxin contamination and the infection can occur either in the field, during post-harvest drying or during curing and storage. Three types of resistance to *Aspergillus* infection and aflatoxin production have been reported in peanut operating at pods (preharvest resistance), seed coat (in vitro seed colonization (IVSC)) and cotyledon levels (aflatoxin production) (Utomo et al. 1990; Nigam 2015). Screening techniques for evaluating resistance of genotypes and advanced generation populations under controlled and field conditions for resistance to seed infection by the fungi and resistance to aflatoxin formation were developed and resistant sources identified. Resistant sources such as ICG 1122, ICG 1326, ICG 3263, ICG 3336 for preharvest infection; PI 337394F, Ah 78223, Monir 240–30 for IVSC resistance; and ICG 10609, ICG 11682, ICG 9610 for aflatoxin production are available, but none of the genotypes are completely free from infection. A basic drawback in identifying resistant lines has been the inconsistency between in vitro resistance screening and field resistance testing (Anderson et al. 1995). Studies have reported a very low correlation (−0.07) between IVSC by *Aspergillus flavus* (IVSCAF) and seed infection in the field indicating independent resistance genetic mechanisms for both types of infection (Utomo et al. 1990; Upadhyaya et al. 1997). For example, in screening trials conducted in the US, it was found that genotypes reported to be resistant to IVSCAF or preharvest aflatoxin contamination performed similar to the susceptible cultivar Florunner in levels of aflatoxin contamination when subjected to an extended period of heat and drought stress (Anderson et al. 1995). Therefore the sampling procedures and screening methods including development of infector plot need to be further

refined to improve uniformity of infection, characterization, and precision of estimation of infection and aflatoxin production in a genotype in a consistent manner (Nigam 2015). Functional genomic tools such as microarray technology, expressed sequence tags (ESTs) are being utilized to identify genes that are expressed or repressed under *Aspergillus* infection (Luo et al. 2005; Guo et al. 2008, 2011) and also those that influence aflatoxin contamination levels (Guo et al. 2008), but developing zero aflatoxin peanuts still remains a dream for peanut researchers across the world. Transgenic technologies involving silencing key genes that regulate aflatoxin biosynthetic pathways holds great promise in this regard.

Peanut proteins are regarded as a major source of allergens and ingestion of seeds is reported to be one of the most serious causes of fatal food-induced anaphylaxis (Yocum and Khan 1994). Peanut-induced anaphylaxis is not a major problem in the Asian and African countries but is more severe in the USA where 0.8% of children and 0.6% of adults are allergic to peanut protein (Sampson 2004; Nigam 2015). Thus, developing non allergenic peanut cultivars is a highly desirable objective among the scientific community. Studies on the nature of the allergen causing compounds have revealed the involvement of about 13 peanut allergens (www.allergen.org) of which Ara h1, Ara h2 and Ara h3 are classified as the major peanut allergens because they are generally recognized by more than 50% of peanut-allergic patients (Koppelman et al. 2001). Specifically, Ara h1 and Ara h2 are recognized by 70–90% of patients with peanut allergy (Burks et al. 1995; Clarke et al. 1998), and Ara h3 is recognized by serum IgE from approximately 44% to 54% of different patient populations with a history of peanut sensitivity (Rabjohn et al. 1999). Screening of genetically diverse peanut germplasms indicated that variability for Ara h1 ranged from 7 to 18.5%, Ara h2 from 5.9 to 13.2%, and Ara h3 from 21.8 to 38.5% of the total protein content of the seed (Koppelman et al. 2001; Kang et al. 2007).

Breeding for reducing or modifying the allergenic proteins through natural or induced

variations or complete elimination through bio-engineering tools such as gene deletion, gene silencing or reduced gene expression are being utilized in peanut improvement programs across the world. Very little natural variation exists in *A. hypogaea* for allergenicity. When the US mini core collection was evaluated for variation in allergen gene expression levels a 2-fold variation was observed in protein amounts for the three major allergens (Kang et al. 2007). Targeting one allergenic component such as Ara h1 for reduced/complete loss of functionality does not seem to have much effect as it is most often compensated for by the presence of other allergens. Molecular tools such as post-transcriptional gene silencing to knock out the production of allergenic protein (Ara h1 and Ara h2) are being employed to mitigate the allergen problem (Dodo et al. 2005, 2008). Recently, genome sequencing of the A-genome progenitor of peanut, *A. duranensis* revealed 21 candidate allergen-encoding genes of which 9 are already reported in cultivated peanut (Chen et al. 2016). Sequence information and functional characterization of these allergen-encoding genes will be useful to identify genetic or medical interventions to allergy mitigation.

2.4.5 Genetic Transformation of *Arachis*

In peanut, the first successful transgenic plant was achieved using the genotype independent method of biolistic/bombardment technique in 1993 (Ozias-Akins et al. 1993). Subsequently, different protocols were developed for transformation, selection and regeneration of transformants which either utilized the genotype independent biolistic approach of targeting embryonic tissues (Chu et al. 2013) or the *Agrobacterium* mediated transformation using shoot regeneration cultures (Sharma and Anjiah 2000). Peanut tissues such as leaf sections, embryo axes, hypocotyls, cotyledonary nodes etc. have been targeted for *A. tumefaciens* transformation with different success rates depending on the culture conditions,

cocultivation protocols and host-pathogen interactions (Holbrook et al. 2011).

Transgenic peanut expressing genes for traits such as resistance to virus, insect and fungus, drought tolerance and grain quality have been developed by different research groups particularly in India, China, and the United States. The first transgenic peanut harboring the herbicide resistance *bar* gene was developed in 1994 (Brar et al. 1994). Another transgenic peanut with tolerance to the herbicide paraquat was developed by the transfer of Bcl-xL gene (Chu et al. 2008). However, high levels of Bcl-xL gene expression was found to be deleterious for plant cells. In the case of virus resistance, transgenic peanuts resistant to TSWV, Peanut Stripe Virus (PStV), Tobacco Streak Virus (TSV) were developed either through transfer of key viral genes in sense or antisense direction (to silence expression of viral proteins) (Li et al. 1997; Yang et al. 1998) or by expressing viral genes in the transgenic plants (Higgins et al. 2004; Mehta et al. 2013). For conferring insect pest resistance, the *cryIEC* δ -endotoxin gene from *Bacillus thuringiensis* was transferred to cultivated peanut and showed effective protection against the larvae of tobacco cutworm (*Spodoptera litura*) (Tiwari et al. 2008). Resistance to the necrotropic fungus *Sclerotinia minor* and *Sclerotinia sclerotiorum*, fungus responsible for causing Sclerotinia blight in peanut, was achieved by transferring the oxalate oxidase gene from barley into three Virginia peanut cultivars (Livingstone et al. 2005). The transformed plants had significantly reduced lesion size when compared to their respective nontransformed control cultivars.

Drought-tolerant peanut plants were reported using *AtDREB1A*, a cis-acting factor that binds to dehydration responsive element (DRE) from *Arabidopsis thaliana* under the control of a stress inducible promoter *rd29A* gene (Bhatnagar-Mathur et al. 2009) and isopentenyl-transferase (*ipt*) gene isolated from *Agrobacterium tumefaciens*, under the control of SARK (a drought-inducible promoter from bean, *Phaseolus vulgaris*) (Qin et al. 2011). IPT is a key enzyme in the biosynthesis of cytokinins, a plant phytohormone which plays important role

in root growth and development. The multigenic trait gene *AtNHX1* from *Arabidopsis* was transformed into peanut and the transformants had enhanced drought and salinity tolerance (Asif et al. 2011; Banjara et al. 2012). The gene *AtNHX1* is an Na⁺/H⁺ antiporter in *A. thaliana* and its over expression increases the ability to sequester sodium into vacuoles, thereby reducing cytosol toxicity, favoring water uptake by root cells and improving tissue retention under stress conditions. Similarly, over expression of *AVPI* (Qin et al. 2013) and *m1D* (Bhauso et al. 2014) gene in peanuts resulted in increased salt and salinity tolerance. *AVPI* encodes a H⁺ pyrophosphatase with proton pump activity on vacuoles, while *m1D* gene encodes the enzyme Mannitol 1-Phosphatase Dehydrogenase that converts mannitol 1-phosphate to mannitol which is accumulated in the transgenic tissue. Although significant progress has been made in transgenic peanuts development, to date no released peanut cultivars are transgenic. Most of the developed products are under evaluation at different containment levels: in vitro, greenhouse and field conditions.

References

- Anderson WF, Holbrook CC, Wilson DM, Matheron ME (1995) Evaluation of preharvest aflatoxin contamination in some potentially resistant peanut genotypes. *Peanut Sci* 22:29–32
- Anderson WF, Wynne JC, Green CC, Beute MK (1986) Combining ability and heritability of resistance to early and late leafspot of peanut. *Peanut Sci* 13:10–14
- Arya SS, Salve AR, Chauhan S (2016) Peanuts as functional food: a review. *J Food Sci Technol* 53(1):31–41
- Asif MA, Zafar Y, Iqbal J, Iqbal MM, Rashid U, Ali GM, Arif A (2011) Enhanced expression of *AtNHX1* in transgenic groundnut (*Arachis hypogaea* L.) improves salt and drought tolerance. *Mol Biotechnol* 49:250–256
- Awad AB, Chan KC, Downie AC, Fink CS (2000) Peanuts as a source of β -sitosterol, a sterol with anticancer properties. *Nutr Cancer* 36(2):238–241
- Banjara M, Zhu L, Shen G, Payton P, Zhang H (2012) Expression of an *Arabidopsis* sodium/proton antiporter gene (*AtNHX1*) in peanut to improve salt tolerance. *Plant Biotechnol Rep.* 6:59–67
- Basu MS, Nagraj G, Reddy PS (1988) Genetics of oil and other major biochemical components in groundnut (*Arachis hypogaea* L.). *Indian J Trop Agri* 6:106–110
- Batal A, Dale N, Caf  M (2005) Nutrient composition of peanut meal. *J Appl Poult Res* 14:254–257
- Bell SL (2008) Peanuts and their classification under the HTSUS. <http://www.cbp.gov>
- Bertioli DJ, Cannon SB, Froenicke L, Huang G, Farmer AD et al (2016) The genome sequences of *Arachis duranensis* and *Arachis ipaensis*, the diploid ancestors of cultivated peanut. *Nat Genet* 48:438–446
- Bhat RV (1991) Aflatoxins: successes and failures of three decades of research. In: *Fungi and Mycotoxins in stored products*, Proceedings of an International conference held at Bangkok, Thailand, 23–26 April 1991, p 80–85
- Bhat RV, Rao RN (1990) Practical guide for prevention and control of aflatoxins in groundnut. National Institute of Nutrition, Hyderabad, India, p 16
- Bhatnagar-Mathur P, Devi MJ, Vadez V, Sharma KK (2009) Differential antioxidative responses in transgenic peanut bear no relationship to their superior transpiration efficiency under drought stress. *J Plant Physiol* 166(11):1207–1217
- Bhauso TD, Thankappan R, Kumar A, Mishra GP, Dobaria JR, Rajam M (2014) Over-expression of bacterial *m1D* gene confers enhanced tolerance to salt-stress and water-deficit stress in transgenic peanut (*Arachis hypogaea* L.) through accumulation of mannitol. *Aust J Crop Sci* 8:413–421
- Bolhuis GG, Frinking HD, Leeuwaugh I, Reno RG, Staritsky G (1965) Observations on the opening of flowers, dehiscence of anthers and growth of pollen tubes in *Arachis hypogaea*. *Netherlands J Agri Sci* 7:138–140
- Brar GS, Cohen BA, Vick CL, Johnson GW (1994) Recovery of transgenic peanut (*Arachis hypogaea* L.) plants from elite cultivars utilizing ACCELL[®] technology. *Plant J* 5:745–753
- Bravo JP, Hoshino AA, Angelici CMLCD, Lopes CR, Gimenes MA (2006) Transferability and use of microsatellite markers for the genetic analysis of the germplasm of some *Arachis* section species of the genus *Arachis*. *Genet Mol Biol* 29:516–524
- Burks AW, Cockrell G, Stanley JS, Helm RM, Bannon GA (1995) Recombinant peanut allergen Ara h I expression and IgE binding in patients with peanut hypersensitivity. *J Clin Invest* 96:1715–1721
- Chen X, Li H, Pandey MK, Yang Q, Wang X et al (2016) Draft genome of the peanut A-genome progenitor (*Arachis duranensis*) provides insight into geocarpy, oil biosynthesis, and allergens. *PNAS* 113(24):6785–6790
- Chu Y, Deng XY, Faustinelli P, Ozias-Akins P (2008) Bcl-xL transformed peanut (*Arachis hypogaea* L.) exhibits paraquat tolerance. *Plant Cell Rep* 27:85–92
- Chu Y, Bhattacharya A, Wu C, Knoll J, Ozias-Akins P (2013) Improvement of peanut (*Arachis hypogaea* L.) transformation efficiency and determination of

- transgene copy number by relative quantitative real-time PCR. *In Vitro Cell Dev Biol -Plant* 49:266–275
- Clarke MC, Kilburn SA, Hourihane JO, Dean KR, Warner JO, Dean TP (1998) Serological characteristics of peanut allergy. *Clin Exp Allergy* 28:1251–1257
- Dodo HW, Konan KN, Viquez OM (2005) A genetic engineering strategy to eliminate peanut allergy. *Curr Allergy Asthma Rep* 5:63–73
- Dodo HW, Konan KN, Chen FC, Egnin M, Viquez OM (2008) Alleviating peanut allergy using genetic engineering: the silencing of the immunodominant allergen Ara h 2 leads to its significant reduction and a decrease in peanut allergenicity. *Plant Biotechnol J* 6:135–145
- Dubey A, Bhattacharya M (2011) Ready to use therapeutic food: a review. *Ind J Pract Pediatrics* 13:1–50
- Duh PD, Yen GC (1995) Changes in antioxidant activity and components of methanolic extracts of peanut hulls irradiated with ultraviolet light. *Food Chem* 54:127–131
- Dwivedi SL, Thendapani K, Nigam SN (1989) Heterosis and combining ability studies and relationship among fruit and seed characters in peanut. *Peanut Sci* 16:14–20
- FAOSTAT (2015) faostat3.fao.org (last accessed on June 25, 2016)
- Firestone D (1999) Physical and chemical characteristics of oils. AOCS Press, Champaign, IL, Fats and Waxes
- Fletcher SM, Shi Z (2014) An overview of world peanut markets. In: Stalker T, Wilson RF (eds) *Peanuts: genetics, processing and utilization*. AOCS Press, Elsevier Inc, London, UK, pp 267–287
- Francisco ML, Resurreccion AV (2008) Functional components in peanuts. *Crit Rev Food Sci Nutr* 8 (8):715–746
- Freeman HA, Nigam SN, Kelley TG, Ntare BR, Subrahmanyam P, Boughton D (1999) The world groundnut economy: facts, trends and outlook. ICRISAT, Patancheru, India, p 52
- Garcia GM, Stalker HT, Shroeder E, Lyerly JH, Kochert G (2005) A RAPD-based linkage map of peanut based on a backcross population between the two diploid species *Arachis stenosperma* and *A. cardenasii*. *Peanut Sci* 32:1–8
- Gautami B, Foncčka D, Pandey MK, Moretzsohn MC, Sujay V, Qin H, Hong Y, Faye I, Chen X, Bhanu Prakash A, Shah TM, Gowda MVC, Nigam SN, Liang X, Hoisington DA, Guo A, Bertioli DJ, Rami Jean-Francois, Varshney RK (2012) An international reference consensus genetic map with 897 marker loci based on 11 mapping populations for tetraploid groundnut (*Arachis hypogaea* L.). *PLoS ONE* 7:1–11
- Gregory WC, Krapovickas A, Gregory MP (1980) Structure variation, evolution, and classification in *Arachis*. In: Summerfield RJ, Bunting AH (eds) *Advances in Legume Science*. Royal Botanic Gardens, Kew, pp 469–481
- Guo B, Chen X, Dang P, Scully BT, Liang X, Holbrook CC, Yu J (2008) Peanut gene expression profiling in developing seeds at different reproduction stages during *Aspergillus parasiticus* infection. *BMC Dev Biol* 8:12
- Guo B, Fedorova ND, Chen X, Wan CH, Wang W, Nierman WC, Bhatnagar D (2011) Gene expression profiling and identification of resistance genes to *Aspergillus flavus* infection in peanut through EST and microarray strategies. *Toxins (Basel)* 3:737–753
- Halward T, Stalker HT, Kochert G (1993) Development of an RFLP linkage map in diploid peanut species. *Theor Appl Genet* 87:379–384
- Hammons RO (1994) The origin and history of Groundnut. In: Smartt J (ed) *The groundnut crop. a scientific basis for improvement*. Chapman & Hall, London, pp 24–42
- Hathorn CS, Sanders TH (2012) Flavor and antioxidant capacity of peanut paste and peanut butter supplemented with peanut skins. *J Food Sci* 77:S407–S411
- Herselman LR, Thwaites FM, Kimmins B, Curtois PJA, Merwe VD, Seal SE (2004) Identification and mapping of AFLP markers linked to peanut (*Arachis hypogaea* L.) resistance to the aphid vector of groundnut rosette disease. *Theor Appl Genet* 109:1426–1433
- Higgins CM, Hall RM, Mitter N, Cruickshank A, Dietzgen RG (2004) Peanut stripe potyvirus resistance in peanut (*Arachis hypogaea* L.) plants carrying viral coat protein gene sequences. *Transgenic Res* 13:59–67
- Holbrook CC, Stalker HT (2003) Peanut breeding and genetic resources. In: Janick J (ed) *Plant breeding reviews*. Wiley, p 297–356
- Holbrook CC, Ozias-Akins P, Chu Y, Guo B (2011) Impact of molecular genetic research on peanut cultivar development. *Agronomy* 1:3–17
- Hong NX, Mehan VK, Lieu NV, Yen NT (1999) Identification of groundnut genotypes resistant to bacterial wilt in Vietnam. *Int J Pest Manag* 45:239–243
- Hong Y, Chen Y, Liang X, Liu H, Zhou G, Li S, Wen S, Holbrook CC, Guo B (2010) A SSR-based composite genetic linkage map for the cultivated peanut (*Arachis hypogaea* L.) genome. *BMC Plant Biol* 10:10–17
- Ibern-Gomez M, Sonia Roig-Perez, Lamuela-Raventos RM, Torre-Boronat MC (2000) Resveratrol and piceid levels in natural and blended peanut butters. *J Agric Food Chem* 48(12):6352–6354
- Jambunathan R (1991) Groundnut quality characteristics. In: *Uses of tropical grain legumes: proceedings of a consultant meeting*, ICRISAT, Patancheru, 27–30 March 1989, p 265–275
- Janila P, Nigam SN (2013) Phenotyping for groundnut (*Arachis hypogaea* L.) improvement. In: Panguluri SN, Kumar AA (eds) *Phenotyping for plant breeding: applications of Phenotyping methods for crop improvement*. Springer, New York, pp 129–167
- Janila P, Variath MT, Pandey MK, Desmae H, Motagi BN, Okori P, Manohar SS, Rathnakumar AL, Radhakrishnan T, Liao B, Varshney RK (2016) Genomic tools in groundnut breeding program: status and perspectives. *Front Plant Sci* 7:289

- Jeandet P, Delaunois B, Aziz A, Donnez D, Vasserot Y, Cordelier S, Courot E (2012) Metabolic engineering of yeast and plants for the production of the biologically active hydroxystilbene, resveratrol. *J Biomed* 2012:579089. doi:10.1155/2012/579089
- Kang I, Gallo M, Tillman BL (2007) Distribution of allergen composition in peanut (*Arachis hypogaea* L.) and wild progenitor (*Arachis*) species. *Crop Sci* 47:997–1003
- Kapil U (2009) Ready to use therapeutic food in the management of severe acute malnutrition in India. *Ind Pediatr* 46:381–382
- Khedikar YP, Gowda MVC, Sarvamangala C, Patgar KV, Upadhyaya HD, Varshney RK (2010) A QTL study on late leaf spot and rust revealed one major QTL for molecular breeding for rust resistance in groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 121:971–984
- Knauff DA, Moore KM, Gorbet DW (1993) Further studies on the inheritance of fatty acid composition in peanut. *Peanut Sci* 20:74–76
- Kochert G, Stalker HT, Gimenes M, Galgario L, Lopes CR, Moore K (1996) RFLP and cytogenetic evidence on the origin and evolution of allotetraploid domesticated peanut, *Arachis hypogaea* (Leguminosae). *Am J Bot* 83:1282–1291
- Koppelman SJ, Vlooswijk RA, Knippels LM, Hessing M, Knol EF, van Reijssen FC, Bruijnzeel-Koomen CA (2001) Quantification of major peanut allergens Ara h 1 and Ara h 2 in the peanut varieties Runner, Spanish, Virginia, and Valencia, bred in different parts of the world. *Allergy* 56:132–137
- Krapovickas A (1969) The origin, variability and spread of the groundnut (*Arachis hypogaea*) (English translation by Smartt J) In: Ucko RJ, Dimbleby CW (eds) *The domestication and exploitation of plants and animals*. Duckworth, London, p 427–441
- Krapovickas A, Gregory WC (1994) Taxonomia del genero *Arachis* (Leguminosae) *Bonplandia* VIII:1–187. (In Spanish). (English translation by Williams DE, Simpson CE 2007). *Taxonomy of the genus Arachis* (Leguminosae). *Bonplandia* 16 (suppl): 1–205
- Latham M, Jonsson U, Sterken E, Kent G (2011) RUTF stuff: Can the children be saved with fortified peanut paste? *World Nutr* 2:62–85
- Leal-Bertioli SCM, Jose ACVF, Alves-Freitas DMT, Mortezoohn MC, Guimaraes PM, Nielen S, Vidiagal BS, Pereira RW, Pike J, Favero AP, Parniske M, Varshney RK, Bertioli DJ (2009) Identification of candidate genome regions controlling disease resistance in *Arachis*. *BMC Plant Biol* 9:112
- Li Z, Jarret R, Demski J (1997) Engineered resistance to tomato spotted wilt virus in transgenic peanut expressing the viral nucleocapsid gene. *Transgenic Res* 6:297–305
- Liao B (2014) Peanut breeding. In: Mallikarjuna N, Varshney RK (eds) *Genetics, genomics and breeding of peanuts*. CRC Press, London, New York, pp 61–78
- Livingstone DM, Hampton JL, Phipps PM, Grabau EA (2005) Enhancing resistance to *Sclerotinia minor* in peanut by expressing a barley oxalate oxidase gene. *Plant Physiol* 137:1354–1362
- Luo M, Liang XQ, Dang P, Holbrook CC, Bausher MG, Lee RD, Guo BZ (2005) Microarray-based screening of differentially expressed genes in peanut in response to *Aspergillus parasiticus* infection and drought stress. *Plant Sci* 169:695–703
- Mehta R, Radhakrishnan T, Kumar A, Yadav R, Dobarra JR, Thirumalaisamy PP, Jain RK, Chigurupati P (2013) Coat protein-mediated transgenic resistance of peanut (*Arachis hypogaea* L.) to peanut stem necrosis disease through *Agrobacterium*-mediated genetic transformation. *Indian J Virol* 24:205–213
- Moncada S, Higgs A (1993) The L-arginine-nitric oxide pathway. *N Engl J Med* 329:2002–2012
- Murthy TGK, Reddy PS (1993) Genetics of groundnut. In: Murthy TGK, Reddy PS (eds) *Cytogenetics and genetics of groundnuts*. Antercept, Andover, UK, pp 144–268
- Nagaraj G (1988) Chemistry and utilization. In: Reddy PS (ed) *Groundnut*. Indian council of Agricultural Research, New Delhi, pp 555–565
- Nagy ED, Guo Y, Tang S, Bowers JE, Okashah RA, Taylor CA, Zhang D, Khanal S, Heesacker AF, Khalilian N, Farmer AD, Carrasquilla-Garcia N, Penmetsa RV, Cook D, Stalker HT, Nielsen N, Ozias-Akins P, Knapp SJ (2012) A high-density genetic map of *Arachis duranensis*, a diploid ancestor of cultivated peanut. *BMC Genom* 13:469
- Nigam SN (2015) Groundnut at a glance. Feed the future innovation lab for collaborative research on peanut productivity and Mycotoxin control, USAID, p 99
- Nigam SN, Upadhyaya HD, Chandra S, Nageswar Rao RC, Wright GC, Reddy AGS (2001) Gene effects for specific leaf area and harvest index in three crosses of groundnut (*Arachis hypogaea* L.). *Ann Appl Biol* 139:301–306
- Olorunju PE, Kuhn CW, Demski JW, Misari SM, Ansa OA (1992) Inheritance of resistance in peanut to mixed infections of groundnut rosette virus (GRV) and groundnut rosette assistor virus and a single infection of GRV. *Plant Dis* 76:95–100
- Ozias-Akins P, Schnell JA, Anderson WF, Singit C, Clemente TE, Adang MJ, Weissinger AK (1993) Regeneration of transgenic peanut plants from stably transformed embryogenic callus. *Plant Sci* 93:185–194
- Pandey MK, Guo B, Holbrook CC, Janila P, Zhang X, Bertioli DJ, Isobe S, Liang X, Varshney RK (2014) Molecular markers, genetic maps and QTLs for molecular breeding in Peanut. In: Mallikarjuna N, Varshney RK (eds) *Genetics, genomics and breeding of peanuts*. CRC Press, London, New York, pp 79–113
- Pensuk K, Jogloy S, Wongkaew S, Patanothai A (2004) Generation means analysis of resistance to peanut bud necrosis caused by peanut bud necrosis tospovirus in peanut. *Plant Breed* 123:90–92

- Qin H, Gu Q, Zhang J, Sun L, Kuppu S, Zhang Y, Burow M, Payton P, Blumwald E, Zhang H (2011) Regulated expression of an isopentenyltransferase gene (IPT) in peanut significantly improves drought tolerance and increases yield under field conditions. *Plant Cell Physiol* 52:1904–1914
- Qin H, Gu Q, Kuppu S, Sun L, Zhu X, Mishra N, Hu R, Shen G, Zhang J, Zhang Y, Zhu L, Zhang X, Burow M, Payton P, Zhang H (2013) Expression of the *Arabidopsis* vacuolar H⁺-pyrophosphatase gene AVP1 in peanut to improve drought and salt tolerance. *Plant Biotechnol Rep*. 7:345–355
- Qin HD, Feng SP, Chen C, Guo YF, Knapp S, Culbreath A, He GH, Wang ML, Zhang XY, Holbrook CC, Ozias-Akins P, Guo BZ (2012) An integrated genetic linkage map of cultivated peanut (*Arachis hypogaea* L.) constructed from two RIL populations. *Theor Appl Genet* 124:653–664
- Rabjohn P, Helm EM, Stanley JS, West CM, Sampson HA, Burks AW, Bannon GA (1999) Molecular cloning and epitope analysis of the peanut allergen Ara h 3. *J Clin Invest* 103:535–542
- Rao MJV, Nigam SN, Mehan VK, McDonald D (1989) *Aspergillus flavus* resistance breeding in groundnut: progress made at ICRISAT Center. In: McDonald D, Mehan VK (eds) Aflatoxin contamination of groundnut. Proc Int Workshop, 6–9 Oct 1987, ICRISAT Center. International crops research institute for the semi-arid tropics, Patancheru, AP, India, p 345–355
- Rathnakumar AL, Hariprasanna K, Lalwani HB (2010) Genetic improvement in Spanish type groundnut (*Arachis hypogaea* L.) varieties in India over the years. *Ind J Oilseeds Res* 27:1–7
- Rathnakumar AL, Singh R, Parmar DL, Mishra JB (2013) Groundnut: a crop profile and compendium of notified varieties of India. Directorate of Groundnut Research, Junagadh, Gujarat, p 118
- Rathnakumar AL, Nigam SN, Muralidharan V, Mishra JB (2015) Groundnut Scenario. In: Rathnakumar AL, Nigam SN, Muralidharan V, Mishra JB (eds) Groundnut at a cross road in India. Mumbai, India, pp 3–4
- Reddy PS (1988) Genetics, breeding and varieties. In: Reddy PS (ed) Groundnut. Indian Council of Agricultural Research, New Delhi, pp 200–317
- Reddy PS, Murthy TGK (1996) Current genetic research on groundnut in India. *Genetica* 97:263–277
- Sampson HA (2004) Update on food allergy. *J Allergy Clin Immunol* 113(5):805–819
- Sanders TH, McMichael RW, Hendrix KW (2000) Occurrence of resveratrol in edible peanuts. *J Agric Food Chem* 48:1243–1246
- Sanders TH, Vercellotti JR, Crippen KL, Hinsch RT, Rasmussen GK, Edwards JH (1992) Quality factors in exported peanuts from Argentina, China and the United States. *J Amer Oil Chem Soc* 69(10):1032–1035
- Seijo GJ, Lavia GI, Fernandez A, Krapovickas A, Ducasse AD, Moscone EA (2004) Physical mapping of the 5 S and 18S-25 S rRNA genes by FISH as evidence that *Arachis duranensis* and *A. ipaënsis* are the wild diploid progenitors of *A. hypogaea* (Leguminosae). *Am J Bot* 91:1294–1303
- Seijo GJ, Lavia GI, Fernandez A, Krapovickas A, Ducasse AD, Bertoli DJ, Moscone EA (2007) Genomic relationships between the cultivated peanut (*Arachis hypogaea*, Leguminosae) and its close relatives revealed by double GISH. *Am J Bot* 94:1963–1971
- Sharma SKK, Anjaiah VV (2000) An efficient method for the production of transgenic plants of peanut (*Arachis hypogaea* L.) through *Agrobacterium tumefaciens*-mediated genetic transformation. *Plant Sci* 159:7–19
- Singh AK, Mehan VK, Nigam SN (1997) Sources of resistance to groundnut fungal and bacterial diseases: an update and appraisal. Information Bulletin no. 50. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, AP, India, p 48
- Singh AK, Subrahmanyam P, Moss JP (1984) The dominant nature of resistance to *Puccinia arachidis* in certain wild *Arachis* species. *Oleagineux* 39:535–538
- Tiwari SP, Ghewande MP, Misra DP (1984) Inheritance of resistance to rust and late leaf spot in groundnut (*Arachis hypogaea* L.). *J Cytol Genet* 19:97–101
- Tiwari S, Mishra DK, Singh A, Singh PK, Tuli R (2008) Expression of a synthetic cry1EC gene for resistance against *Spodoptera litura* in transgenic peanut (*Arachis hypogaea* L.). *Plant Cell Rep* 27:1017–1025
- Upadhyaya HD, Sharma S, Dwivedi SL (2011) *Arachis*. In: Kole C (ed) Wild crop relatives: genomic and breeding resources: legume crops and forages. Springer publishing house, London, New York, pp 1–20
- Upadhyaya HD, Nigam SN, Mehan VK, Lenne JM (1997) Aflatoxin contamination of groundnut—prospects of a genetic solution through conventional breeding, p. 81–85. In: Aflatoxin Contamination Problems in Groundnut in Asia: Proceedings of the First Working Group Meeting, 27–29 May 1996, Ministry of Agriculture and Rural Development, Hanoi, Vietnam (V.K. Mehan and C.LL. Gowda eds.). Patancheru 502 324, Andhra Pradesh, India: International Crops Research Institute for the Semi-Arid Tropics
- Utomo SD, Anderson WF, Wynne JC, Beute MK, Hagler WM Jr, Payne GA (1990) Estimates of heritability and correlation among three mechanisms of resistance to *Aspergillus parasiticus* in peanut. *Proc Amer Peanut Res and Educ Soc* 22:26
- Valls JFM, Simpson CE (2005) New species of *Arachis* (Leguminosae) from Brazil, Paraguay and Bolivia. *Bonplandia* 14:35–63
- Varshney RK, May GD (2012) Next-generation sequencing technologies: opportunities and obligations in plant genomics. *Brief Funct Genom* 11:1–2
- Varshney RK, Bertoli DJ, Moretzsohn MC, Vadez V, Krishnamurthy L, Aruna R, Nigam SN, Moss BJ, Seetha K, Ravi K, He G, Knapp SJ, Hoisington DA (2009) The first SSR-based genetic linkage map for

- cultivated groundnut (*Arachis hypogaea* L.). *Theor Appl Genet* 118:729–739
- Woyengo TA, Ramprasath VR, Jones PJ (2009) Anti-cancer effects of phytosterols. *Eur J Clin Nutr* 63 (7):813–820
- Yang H, Singsit C, Wang A, Gonsalves D, Ozias-Akins P (1998) Transgenic peanut plants containing a nucleocapsid protein gene of tomato spotted wilt virus show divergent levels of gene expression. *Plant Cell Rep* 17:693–699
- Yen GC, Duh PD (1994) Scavenging effects of methanolic extracts of peanut hulls on free-radical and active-oxygen species. *J Agri Food Chem* 42 (3):629–632
- Yocum MW, Khan DA (1994) Assessment of patients who have experienced anaphylaxis: a 3-year survey. *Mayo Clin Proc* 69:16–23
- Yu SL (2011) *Peanut genetics and breeding in China*. Shanghai Scientific and Technology Press, Shanghai, China
- Zhou GY, Liang XQ (2002) Analysis of major-minor genes related to resistance to infection by *Aspergillus flavus* in peanut. *J Peanut Sci* 31:11–14
- Zhou GY, Liang XQ, Li YC, Li XC, Li SL (1999) Evaluation and application of introduced peanut cultivars for resistance to *Aspergillus flavus* invasion. *J Peanut Sci* 32:14–17
- Zhou XZ, Xia Y, Ren X, Chen Y, Huang L, Huang S, Liao B, Lei Y, Yan L, Jiang H (2014) Construction of an SNP based genetic linkage map in cultivated peanut based on large scale marker development using next-generation double-digest restriction site associated DNA sequencing (ddRADseq). *BMC Genom* 15:351