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Review paper

Seed Development in Groundnut - Floral Biology and Peg Development

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Abstract: Groundnut (*Arachis hypogeae* L.) is a semi-determinate plant in which flowering continues for a long period depending on the habit group or botanical types. The inflorescence varies among different types, whereas, flower is typically papilionaceous, zygomorphic and self-pollinating (clestogamous). Since, groundnut possesses a geocarpicovary, understanding the physiology of flowering, peg and pod development are important for planning seed production. The inheritance of flower on main stem inflorescence is regulated by two sets of duplicate loci with epistatic action, while sequential flowering is regulated by duplicate pair of recessive genes (i.e., monogenic-recessive to alternate). In Spanish type, flower appears relatively early and has a broader first flowering peak, whereas, in Virginia type flowering is delayed with multiple peaks. Floral induction is controlled by both external as well as internal stimuli and regulates the development of reproductive primordia. The most sensitive stage for induction of flowering is reported to be around three days prior to bloom. Further, the onset of flowering including peg/pod development is controlled by intricate genetic network in response to extrinsic factors, i.e., day length, temperature and intrinsic factors, i.e., hormones, and cross-talks between them, including involvement of endogenous signaling molecules. In addition, groundnut peg has the ability to suspend its development during the period of soil moisture-deficit and resume pod development after the relief of stress. The geotropic nature of peg has a peculiar physiology to fulfill the requirement of darkness for the development of fertilized ovule into pod and seed. For this purpose the peg, along with the fertilized ovary carried at the tip, penetrates the soil under optimum moisture condition. In addition, variation in pod number in groundnut is mainly associated with timing of flowering and the initial rate of flower production. It is a well- established fact that extended exposure to high temperature and water-deficit conditions could reduce flowering and peg numbers as well as pod formation, thus limiting the reproductive efficiency. Such flowering behavior in groundnut results variations in maturity of pod/seed leading to seeds of different size and weight at the final harvest, and resulting in poor quality. Hence, understanding the environmental influence on floral biology and peg development is important for quality seed production in groundnut.

Keywords: Groundnut, Floral biology, Peg development

INTRODUCTION

Flowering is a high energy driven process, as flowers after anthesis play the primary role in seed formation. Groundnut flowering behavior is indeterminate and flower production continues until the last phase of growth and development. Different groups of groundnut have flowering peaks at specific intervals. The flowers produced after the productive period are wasted. This habit is more prevalent in Virginia and less in Spanish and Valencia types. Such behavior of plants creates a competition between reproductive and vegetative parts for the photosynthates. As a consequence, the estimated yield loss could be as high as 12-20% due to low pod set or low reproductive efficiency [1]. The flower shape, size and colour in different groundnut types, including the wild *Arachis* species are more or less similar. Variations in flowering pattern and pod and seed characteristics are documented by Krapovickas and Gregory [2] and Nigam et al. [3]. The early maturing Spanish type flowers within 10-15 days after emergence while long duration Virginia type flowers in 30-45 days. In addition, spreading and semi-spreading Virginia types invariably produce higher number of flowers and seed yield as compared to early maturing erect Spanish and Valencia types. In early maturing varieties peak flowering period is relatively shorter and flower shedding may be higher during early as compared to the later season. Among the different types, total number of flowers produced are lesser in Spanish (bunch type) but the number of pegs and pods developed may be higher than Virginia types (spreading and semi-spreading). The peak flowering in one of the wild *Arachis* species and a Spanish type cultivar is shown below (Fig. 1A and B).

Figure 1. Wild *Arachis* species in flowering (A) and Spanish type cultivar (B) at DGR, Junagadh, Gujarat, India

In addition to genetic variations, peg and pod developments are influenced by both external and internal factors. Hence, influence of internal stimuli and external environmental factors are necessary to our understanding for developing climate resilient varieties. In groundnut, it is necessary to understand the requirement of heat unit for development of pod to a healthy seed. As based on heat unit requirement for various stages of plant growth and development, heat unit index could be developed to account for variations (in calendar time) from sowing to seed maturity. Under field conditions, sometimes, it may not be so accurate due to compounding effects of factors other than temperature [4].

Floral biology

Different botanical types of groundnut possess different types of inflorescence. Virginia type has a simple inflorescence, expanding slightly in length during maturity. Whereas, in Spanish the inflorescence is compound and extends moderately. On the other hand, in Valencia the inflorescence is simple, but may elongate to form a conspicuous long branch. Branching is dimorphic, with vegetative branches and contracted reproductive branches. The contracted reproductive branch or inflorescence is formed slightly at both cataphyll and ordinary leaf axils on vegetative branches, and some time forms at higher nodes on the central stem. Each inflorescence bears 2-5 flowers; short branches develop in axils of simple bracts that occur along central axis of the inflorescence and terminate after production of one leaf, the bifid bract, from the axis of which flower is borne. Groundnut flowers are basically sessile consisting of a 4-6 cm long tubular hypanthium, i.e., fused lower part of the calyx, corolla and stamina tube, the top of which bears expanded lobes of 5 sepals and petals. The flower colour varies from yellow to orange to dark orange or garnet, and in rare cases, it is white or creamy white. Each flower consists of five petals bright yellow to yellowish-orange with reddish striations. The five petals differ in shape and size such as the upper one form a large banner, two smaller than the banner form lateral wings, and a keel formed by two fused petals. The keel petals enclose 10 or 9 monadelphous stamens, androecium and gynoecium or pistil. In general, two stamens are reduced to staminodes and become sterile which are represented by filaments. The remaining eight are dimorphic with 4 long and 4 shorts. Normal flowers contain either a feather or club-like stigma, the pistil consists of a single ovary surrounded by base of the hypanthium, the ovary is about 1.5 mm long and 0.5 mm wide, and has 2 to 6 ovules. The stigma is club shaped, usually at the anther level or protruding slightly above. The style is pollen receptive

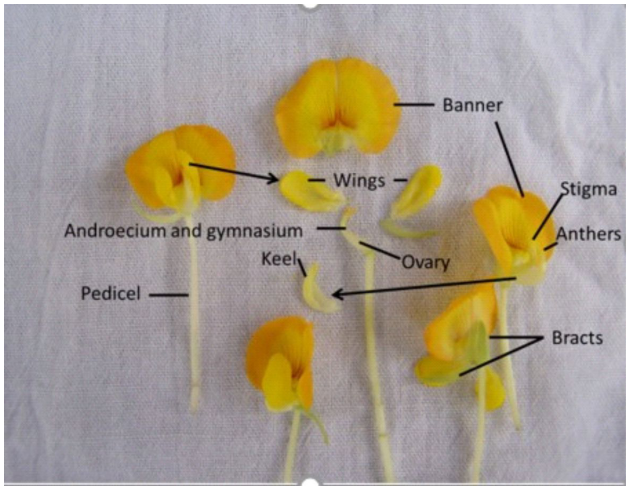

Figure 2. Parts of groundnut flower

for much of its length. The flower bud remains between 6 and 10 mm long 24 h before anthesis while during the day, the hypanthium elongates slowly and the bud attains a length of 10-20 mm. During night hours elongation of hypanthium is faster and flower reaches the maximum length of 50-70 mm at anthesis. Flowers open normally at sunrise, but low temperatures and poor radiation delay this process. In groundnut, genetic variations exist in anther dehiscence, for example, it may dehisce 7-8 h before the flower opens in some genotypes while in others, they may do so even at flower opening.

Floral genetics

Cultivated groundnut is an allotetraploid (2n=40) species, whereas most wild groundnut relatives in the same genus are diploids (2n=20). Crosses among elite cultivars are practiced to develop modern varieties with desirable traits such as higher yield and biotic and abiotic stresses tolerance including improved nutrition quality [5]. The king petal shape is monogenic character and is determined by boat-shape dominant to broad or scoop-shape [6]. Pod size is determined by large-pod being dominant to small and small-pod dominant to large pod duplicate genes [7]. Pod constriction is digenic with absence being dominant to its presence. It is controlled by three nuclear genes and one cytoplasmic factor complimentary duplicate [8]. Large seed is dominant to small seed size controlled by five pairs of gene [9]. Long seed shape is dominant to short (digenic) and flat-end of seed is dominant to smooth. Further, sub-species of *hypogaea* and *fastigiata* showed significant differences for quantitative traits except for numbers of pods per plant and seed yield. Major traits that accounted for the variation include days to the first flowering, days to 50% flowering, number of pods plant^{-1} and shelling percentage. Various studies have shown that inheritance of flower on main stem inflorescence is controlled by two sets of duplicate loci with epistatic action while sequential flowering is controlled by duplicate pair of recessive genes, monogenic-recessive to alternate [10]. In addition, corolla colour is determined by dark-dominant to light-orange incomplete-dominant to white-yellow-dominant to white controlled by duplicate genes [15 yellow:1white) yellow-incomplete-dominant to white or controlled by additive gene with 9 yellow, 6 pale yellow and 1 white colour [11]. The groundnut collection also offers wide seed coat colour diversity which affects the crop marketability [12]. In addition, plant growth habit, leaf size and flowering were reported to be controlled by independent gene [13]. Understanding of floral genetics is important for better planning in plant breeding strategies. This explains the inheritance mechanism of floral parts that is essential for enhancing hybridization and ultimate breeding efficiency. It is believed that genetic diversity in cultivated groundnut is narrow; therefore, ample allelic diversity among wild relatives has spurred interest in using interspecific hybrids to broaden the genetic base of cultivated groundnut [14]. Moreover, hybridization programmes need special knowledge and skill for selection of parents and emasculation and crossing processes. In this regard considerable progress has been made in the past several decades in genetics and plant breeding of groundnut [15, 16, 3].

Floral induction

The onset of flowering in plants is controlled by an intricate genetic network in response to environment, such as, day length, temperature and endogenous signals (i.e., hormonal status) and carbohydrates concentration, i.e., trehalose-6-phosphate [17] this initiates growth within the buds in regions known as meristems. Later on meristemic cells start division followed by elongation. These processes produce tissues that soon develop into specific organs. The reproductive meristems give rise to floral organs that ultimately produce fruit and seed. Flowers are borne on inflorescence located in the axils of the leaves, and never at the same node as vegetative branches. In addition, due to presence of very short internodes on some plants, it may appear as if they are emerging from the same branch. After initiation of flower primordial, it usually opens after 18-21 days and developing flower bud usually become visible 36 to 48 hours before the flower bud open. In general, base temperature for time to first-flower is estimated as 10.8°C while total cumulative degree days for flowering are reported approximately 538 (°d). Whereas, Bagnall and King [18] reported that the first flower appearance in a linear thermal-time model, if mean temperatures above 30°C is excluded. In addition, Spanish type exhibited a higher base temperature (approximately 13.6°C) than either Valencia (12.5°C) or Virginia (11.4°C) for flower initiation. Thus, the time to first flower is little affected by photoperiod, whereas, temperature has a major and positive impact.

In groundnut, flowering is generally reported in four stages, the pattern of which depends upon cultivar and the environment. In Spanish and Virginia types, about

65 and 79% of flower production is reported to be during the first 5 weeks after appearance of the first flower. Groundnut produces much more flowers than the number of developed pods, as the number of flowers produced plant^{-1} may range between 40 and 250 in Virginia and 98-137 in Spanish types [19, 1]. It is estimated that about 40% of the flowers produced during the peak flowering period are converted into pods. As far as reproductive efficiency is concerned, the pattern of flowering (i.e., number of flowers produced during different flowering peaks) is more important than the total number of flowers produced throughout the life span. Coffelt et al. [20] have calculated groundnut flowering behaviour and reproductive efficiency by counting total number of flowers produced up to effective period and their conversion into mature pods. Fluctuations in flowering patterns have also been reported with alterations between high and low frequencies during major flowering period [21]. Thus flowering pattern has a close relationship with pegging and ultimate productivity. It was also reported that number of double-seeded mature pods plant^{-1}, weight of double-seeded mature pods plant^{-1}, number of mature seeds plant^{-1}, mass of mature seeds plant^{-1} were highly influenced by flowers retained between 25 and 55 days after sowing [22]. Experiments on removal of flowers during peak flowering period exhibited significant increase in the intensity of flowering [23, 24]. In addition, higher planting density and blooming period (flowering rate) is negatively associated with plant density under field conditions [25]. There is a benefit in closer spacing for suppression of late flowers, which may contribute to synchronize flowering [26].

Flowering and photoperiod

Plant response to relative length of the day and night to growth and development is known as photoperiodism, which is the sensitivity of the plants to length of the dark period (night) and not the length of the day, such as, long nights induce flowering in short-day plants and inhibit in long-day plants. On response of plant to photoperiod and physiology of flowering there are contradictory reports in case of groundnut. For example, there are reports mentioning that phenology of groundnut is not affected by the day length, concluding that groundnut may be considered as day-netural [27, 28]. On the other hand, it was demonstrated that pod yield was significantly influenced by the day length [29]. This was attributed to the fact that long days promote vegetative growth at the expense of reproductive growth, thus resulting into poor pod filling and HI [30, 31]. There are reports that the day-length affects time to first-flower and either long or short days may hasten the first-flower appearance [32, 33]. Bell et al. [34] reported that photoperiod effects could be seen only at a very low quantum.

Growth regulators and flowering

Growth regulators are chemical substances that play important role in determining the growth and development of the plant including physiology of flowering. In addition, application of plant growth regulators to crops could modify hormonal balance and growth to enhance yields. Hormonal balance is also needed to enhance the tolerance to biotic and abiotic stresses. Both laboratory and field studies have shown that foliar sprays of phenolic compounds eg., β-napthol-1-amino, 4-sulphonate in the concentration of 100, 150 µg/ml and a mixture of aliphatic alcohols-C-24 to C-34 (1 µg/ml) at 30 and 37 days after emergence may be effective in increasing flower production, such as, total number of flowers produced plant^{-1} and number of flowers produced during effective period (i.e., initial 3 weeks) [35]. It was concluded that these compounds were effective in inducing and establishing the early potential-sink. This enhances efficient mobilization of assimilates for a longer pod filling period. Foliar spray of Ethrel, Chlorocholine chloride (CCC), Maleic Hydrazide (MH), Naphthalic Acetic Acid (NAA) and Mepiquat chloride (PIX) in different concentrations at 60 days after sowing is effective in increasing the pod weight and ultimate seed yield. Also, synchronized flowering leads to reduction in number of immature pods, and increase in number of double seeded pods, contributing to higher pod yield [22]. It is well supported by the laboratory experiments that shoot potential of groundnut genotypes was influenced by application of BAP (6-benzylaminopurine). Also, flowering was observed in var. PBS24030 by applying 1 mg LG1 NAA in the growth media. In addition, application of cytokinins induced flower buds in cotyledons with embryonic axis cultured with Blaydes' medium, the frequency of flower bud induction increased with increasing concentrations of cytokinins. In the same experiment, growth regulators IAA, NAA, GA_3 and ABA failed to induce flower buds in independent treatments, however, lower concentrations of IAA and NAA in combination with cytokinins exerted a positive influence on flowering. In addition, 6% of the induced flowers resulted in gynophore development and ultimately pod formation when cultured under complete dark conditions

in modified MS medium supplemented with kinetin [36]. Role of the brassinosteroids in groundnut flowering is also suggested by Verma et al. [37].

Influence of high temperature and water-deficit on flowering

Various environmental factors such as temperature, humidity and sunshine may influence plant growth and phenology, especially the time taken to initiate and open the first flower. Higher temperature and drought are directly associated with increased canopy temperature, which may result in decrease supply of photosynthates, heat-shock, cell injury and/or decreased growth rate, less flowering and ultimately low yield. Continuous high temperature during later stages of vegetative phase can decrease flower production due to its effect on branching and overall growth. Also, prolonged stressed environment may cause flower drop due to abscission. On the other hand, an increase in the rate of flower production followed by episode of higher temperature(>35°C) showed increase in cumulative number of flowers produced as compared to the number of flowers produced at optimum temperature (28°C) [38]. It is also reported that there is reduction in pod yield under high temperature during flowering and peg formation [39, 40, 41, 42]. In addition, Talwar et al. [43] reported that flower buds are sensitive to high temperature, especially 3 to 5 days, prior to anthesis. It is also concluded that sensitivity to high temperature stress extends from 6 day before anthesis until 15 days after flowering, therefore, flowers formed only during the first 3 weeks are usually considered beneficial [44, 45, 46]. Thus to calculate pod yield in relation to the flower production, percentage of flowers converted to pods is crucial rather than the total number of flowers produced, as variation in fruit number in groundnut genotypes is mainly associated with timing of flowering and the initial rate of flower production [47]. Thus, timing of flowering, rather than heat tolerance or susceptibility is the main parameter for calculating mature pods number.

It is clear that male and female flower organs in groundnut are very sensitive to high temperature, especially when temperature exceeds beyond 30°C [48]. Most likely gametophyte development and anther dehiscence were found to be susceptible to high temperatures [49]. It is also postulated that high temperature stress is quantitatively related to floral bud temperature and can regulate flower production and fruit-set [50]. Specifically, the influence of high temperature during flowering is attributed to the exposure of flower buds coinciding with microsporogenesis leading to low pollen viability, poor anther dehiscence, and male sterility [51]. Further, this is attributed to early degeneration of tapetal layer [52] and depletion of carbon reserves in developing pollen [53]. In conclusion, high temperature effects on grain legume are attributed to various metabolic and physiological processes, such as, flower abortion, pollen and ovule infertility, impaired fertilization, and reduced seed filling, leading to smaller seeds and poor yields [54].

In addition, water-deficit stress is always coupled with high temperature thus influence the basic physiological processes of plant growth and development. In groundnut water-deficit stress during flowering is reported to be detrimental to number and size of flowers, maintaining shape and size of floral organs, thus resulting in loss of flowers and leading to the production of immature pods. Moreover, high temperature may operate to modify crop development in two directions depending on time, type and severity of the stress. In addition, water-deficit stress during reproductive growth may result in slower or quicker achievement of maturity depending on the time of the onset of stress [55]. Compounding and confounding effects of high temperature and water-deficit stresses in groundnut has been reviewed by Kakani et al. [56]. A study with large number of genotypes assessed for pod yield and physiological parameters under high temperature stress and non-stress environments recorded significant variability for pod yield [57]. Thus it is well known that soil-moisture deficit stress during different crop growth stages reduces total number of flowers. On the other hand, a transient water-deficit stress during vegetative phase followed by two frequent irrigations within interval of one week may enhance synchronization in flowering peaks and the ultimate productivity. Thus, higher productivity through synchronized flowering can be achieved in Spanish types [39]. In addition, it is reported that there are memories of stress events can be inscribed and inherited to offspring through a process known as transgenerational stress memory, for example, groundnut grown under controlled water availability exhibited increased seed quality and vigour in next generation plants [58].

Pollination and fertilization

Groundnut is self-pollinating crop and does not need to attract bees or other insects for pollination and can be grown in geographical areas where pollinators are scarce or absent. Groundnut pollen grains are smooth, oval and

sticky, while pollen development is an important aspect for successful pollination. As pollen grain has various phases of hydration and dehydration which are mainly controlled by water homeostasis with five different phases but studies on this aspect are limited. During male gametophyte development the specific water levels are maintained using various structural, physiological and molecular mechanisms. These five phases differ in optimum hydration levels as needed for the specific biological function. It is important to note that pollen grain may also use this mechanism for coping with stressful environmental conditions as usually the seed does. Hence, there are similarities between developing seed and pollen, such as during maturation, both accumulate non-reducing sugars and late embryogenesis abundant (LEA) proteins indicating that these two types of molecules interact in the formation of a glassy state [59]. Since, dehydration cause anther to dehisce and the pollen grain to function its biochemical processes at a minimum rate. In addition, the molecular mechanisms involved in pollen water homeostasis include water channels that may facilitate water movement, on one hand, and mechanisms that enable it to retain water such as the accumulation of specific sugars and proteins. It is presumed that aquaporins might play a significant and important role during pollen rehydration on the stigma. Functionally characterized aquaporin genes that are highly and selectively expressed in mature pollen of *Arabidopsis thaliana* have already been reported. In a proteomic study of pollen, there was considerable overlap in some of the major proteins present in mature pollen grains and seed [60]. As pollen also undergo dehydration and hydration processes to complete anthesis or pollination, the role of aquaporins might be equally interesting to understand their functioning in groundnut. In addition, pollen viability test is often applied at high temperature or any other stressful environment [61]. Relative humidity also plays very important role in pollen germination and fertilization and it is reported that foliage and pod fresh and dry weights, total seed yield, HI and seed maturity. It is reported that gynophores grew more rapidly at 85% than at 50% RH [62].

Groundnut pollen remains viable at 90-95% humidity and at high temperature cycle, i.e., 32/22°C and 36/26°C, and viability may decrease to near about zero at 44/34°C day and night cycle [63]. Pollen matures approximately 6 to 8 hours before anthesis, but pollination does not usually occur until at or near flower opening (anthesis). The pollen grain after reaching the stigma starts germination and sends out a pollen tube, which grows down the style, through the micropyle and into the embryo sac, with the tube nucleus closely following the tube apex downward. The tube nucleus soon degenerates, but the two pollen sperm cells enter the embryo sac, one fusing with the diploid (2N) polar nucleus to form a triploid (3N) endosperm nucleus and the other fusing with egg cell to form a diploid zygote or fertilized egg, and endosperm does not persist until maturity. Embryo and endosperm result from a complex interaction of genes, the megagametophyte, the haploid female gamete and the diploid sporophytic body of the mother plant. After fertilization a mature pod develops in about 60 days whereas low humidity during pod development is detrimental to embryo development [64]. Groundnut flower opens early in the morning around 06:00 h and fertilization is completed before mid-day. After fertilization the flower droops. Stigma becomes receptive for about twenty-four hours prior to anthesis and its receptivity persists for about 12 h after anthesis. Fertilization usually occurs 6 h after pollination. The calyx tube and flower wilt within 6-8 h normally. Low temperatures adversely affect the anthesis and delayed by 12 to 18 h in winter season (i.e., ≤10°C). The actual embryogenesis, starts with the formation of a single-cell zygote which ends in the heart stage and at this stage all embryo structures have been formed [65]. When first phase of embryo growth is completed, cell division in the embryo gets arrested [66]. After fertilization, the young embryo undergoes four or five divisions, and then becomes dormant. Simultaneously, cells at the base of ovary become active (intercalary meristem) and begins to grow a peg or ovary stalk, which is positively geotropic. The differences in pod development in groundnut and other legumes are mainly because of the sensitivity of pro-embryo to phytochrome, geocarpic nature of gynophores, calcium uptake by developing pod, non-chlorophyllous pod and nature of seed dormancy.

Peg/pod development

Darwin studied the geocarpic nature of gynophores in groundnut and mentioned in his book “The power of movement of plants” (1880) that the movement of gynophore is not light dependent. Later on, it was demonstrated that growth of intercalary meristem is promoted by light and ceases only when gynophores reach under the soil in dark condition. The intercalary meristem is responsible for elongation of gynophores or peg and when its growth is ceases only then development

of embryo starts. Thus, embryo growth is inhibited under light which is a reversible process, however, growth of intercalary meristem is irreversible process. After fertilization, growth of ovule and embryo is light-dependent, for example, white, red or blue radiation inhibits ovule growth while exposure to darkness or far-red light stimulates it, especially, during the first 10 days. It is also demonstrated that there is a photoreceptor which regulates ovule growth, i.e., phytochrome located in maternal ovular tissue and transmit developmental signal to the embryo [67, 68]. Therefore, after fertilization, peg formation takes place and exhibit positive geotropism to keep the embryo below soil for further growth. In addition, failure of peg penetration into the soil leads to formation of aerial pods. In a study, flower bud was emasculated during the early and in the late afternoon, and no significant difference in their ability to form pegs was found. Also, studies on emasculation and pollination showed that manually pollinated flowers are capable of producing more pegs than naturally self-pollinated flowers. This indicated that natural pollination by itself is not adequate for optimum production of pegs [69]. In addition, groundnut has a unique characteristic that ovaries of pollinated flowers can remain dormant for several weeks and resume active seed development when environmental conditions become favorable [21].

As peg elongates, a cap of cells forms next to the withered style that protects ovary and direct it into the soil, similar in function to the root cap. After the developing ovary gets pushed a few centimeters into the soil, downward elongation of peg ceases. The ripening ovary becomes oriented parallel to the ground surface where it completes its development. The vascular system of the mono-carpellary gynoecium with 10 well differentiated traces and a few cross links probably represents a precocious development of post-fertilization vasculature of fruit wall. During sub-soil fruit development, the ovary wall develops a prominent spongy inner zone which finally disappears and a peripheral zone forms the mature fruit wall. Peg length always remains under control of both genetic and environmental conditions and ranges from 1 to 2 cm to 1m in wild *Arachis* species. The long weak pegs of most wild *Arachis* species complicate use of these taxa for human food or animal forage. Further, with the advancement of knowledge on groundnut genome, discovery of genes/variants for traits of interest and integration of marker assisted breeding for selected traits. The integration of genomic tools into the breeding process accompanied with increased precision of yield trialing and phenotyping may increase the efficiency in release of improved varieties [70].

Also, a causal relationship between effects of high humidity and growth regulator status of developing fruit was reported. In addition, plants grown at 85% RH showed greater leaf area and stomatal conductance, flower anthesis appeared 3 days earlier. In addition, it was also reported that anthesis could be higher at 85% than at 50% RH. Moreover, the ongoing climate change also affects photoperiod sensitivity [71]. It could be concluded that under changing climatic scenario, higher temperature stress may be a severe limiting factor to enhance productivity. It has been proved experimentally that plants shifted from low to high humidity conditions also set higher percentage of pegs, maintain higher rate of ethylene production by 2-centimeter peg sections, a higher growth rate of intact pegs. Also, such plants maintain a higher mean content of gibberellins than plants transferred from high to low humidity conditions. Maximum ethylene production occurred during initial stages of peg growth, i.e., 1-5 mm sections, and gibberellin content was recorded higher in peg sections [72].

Peg penetration

The fertilized ovule penetrates the soil layer with the help of gynophore (i.e., peg) and pod development take place under dark conditions in the soil. For illustration, after fertilization, the flower stalk curves downward and developing pod is forced into the soil by proliferation and elongation of cells present at the base of ovary. It is important to note that the gynophore is sensitive to light, touch, and gravity. During the process of development of gynophore, the cells beneath ovary begin to divide, producing a peg that forces ovary into the soil. In soil the rates of growth of vertically and horizontally oriented gynophores was reported in the region of maximum extension due to elongation and known as the central elongation zone, located on an average at 2-5 mm from the tip. In the first 0-4 h after horizontal reorientation, i.e., gravistimulation, new zones of growth emerge on the upper surface, while the elongation zone of the lower side decreases in size and magnitude. Ovule after fertilization develop pegs within 6 days, thereafter pod development starts between 16 and 18 days depending on the position of the peg to enter into the soil. But the ratio of the number of mature pods to the total number of

flowers was reported to be very low (i.e., about 8-17% only) [1]. After penetration of peg into the soil pod begins to expand rapidly until it reaches dimensions that are characteristic of the individual cultivar [38]. Pod development commences 5-6 days after the peg penetrates the soil and after that peg elongation stops.

The anatomy and morphology of developing ovary and pod have been described adequately in literature [73]. A study conducted by Thompson [68] on determination of the nature of the photoreceptor that controls light-dependent development of groundnut ovule and embryo. When light sources were altered after the first 10 days of culture, those ovules exposed first to darkness or far-red radiation began to increase in volume which then ceased after subsequent exposure to white, red or blue radiation. Likewise, if white, red or blue radiation was given during the first 10 days, ovule development was inhibited and could be stimulated by exposure to darkness or far-red light. The red/far-red reversibility indicates that the photoreceptor that regulates ovule growth is phytochrome and that the maternal ovular tissue appears to be the site of photoreception, which may then transmit some developmental signals to the embryo. The first step of peg initiation is to sense gravity and bending downward [74]. Initially, the emerged aerial peg does not show any changes in the developing embryo as mitotic division is arrested with the embryo remaining at the proembryo stage. The intercalary meristem situated at the base of the ovary divides rapidly resulting in peg elongation and implantation of the arrested embryo into the soil. When peg tip penetrates the soil vertically, it reorients horizontally and perceives signals that prompt the resumption of embryo cell division thus facilitating geocarpic pod development. It is important to note that the perception of mechanical stimulus and darkness is essential for transformation of the peg into a pod. Without these signals the embryo may get aborted. The anatomy of peg typically resembles the shoot [75]. On the other hand, anatomy of unfertilized peg varies as compared to the fertilized peg. In this case, the former lacking starch granules. Though the anatomy of peg resembles with stem, its behaviour and function changes after soil penetration and shift with resemblance to root [74]. Aerial peg consists of multicellular trichomes of five to six cells in length of which the terminal cell elongates compared to the first four to five proximal cells. After the peg penetrates the soil, unicellular hairs similar to root hairs develop abundantly on the subterranean peg surface. The especial features of aerial peg are smooth epidermis and the presence of numerous stomata and lenticels, gradually disappear and become obscured by tufts of hairs present in subterranean peg [76].

Aerial peg is self-sufficient for energy production because it possesses chlorophyll o/r and machinery for photosynthesis. The considerable photosynthetic activity of the sub-epidermal parenchyma tissue is evident from the presence of stomata, and high starch content of aerial peg [77].In addition, proteome mapping of groundnut reproduction and pegging stages identified expression of approximately 34 photosynthesis-related proteins in the aerial peg such as photosystem II type I chlorophyll a/b-binding proteins, oxygen evolving enhancer protein 1/2, rubiscoactivase, plastocyanin, representing a sub-set of core proteins involved in photosynthesis [78].The number of these photosynthetic proteins drastically reduces in subterranean peg/pod. On the other hand, these photosynthetic proteins, other multiple energy metabolisms related proteins such as glycolytic pathway proteins-fructose bisphosphatealdolase and triosephosphateisomerase have been identified in the subterranean peg [79].

Amyloplast accumulation and spatial distribution

Soon after fertilization, the previously gravitropic peg starts to accumulate amyloplasts and responds to gravity [80]. A strong constriction or secondary gynophores may develop between seed compartments, but it is usually not seen in cultivated groundnut [81]. These starch-rich amyloplasts are denser than the cytoplasm and act as statoliths by sedimenting material according to gravity [82]. This gives peg, the information on its orientation in the gravity field and hence the direction in which tropic growth must occur to reach the soil. On the other hand, the unfertilized peg has neither visible amyloplasts nor responds to gravity [77]. Once the ovary is adequately buried into the soil, embryo development is resumed and fruit expansion starts. Supply of sugars, proteins and inorganic nutrients other than calcium to the developing pod is ensured through the gynophores. There is a strong correlation between amyloplast development and competence of the peg to bend with gravity vector. Amyloplasts are located in starch sheath in the apical region (2-8 mm) of the peg tip which includes the main elongation zone near intercalary meristem [76]. These cells are therefore the gravity-sensing cells or statocytes of the peg. Usually, amyloplasts are sedimented at the

apical surface of the peg statocytes, i.e., relative to the peg tip, in vertically-oriented pegs; however, following reorientation of peg to the horizontal, the amyloplasts come to rest on the lateral wall of the statocyte, i.e., to the new lower surface of the starch sheath cells just before the formation of gravitropic curvature. In groundnut, application of exogenous gibberellic acid (GA) and kinetin was able to de starch the peg resulting in starch less amyloplasts and an almost complete loss of gravitropic response [77]. These studies provide strong evidence for the amyloplast assisted peg gravitropism.

Molecular biology of peg development

Peg and pod development involves several genes related with lipid metabolism and signaling such as phospholipid transporters, phospholipid-transporting ATPase, lipid kinase, sterol binding protein, calcium-dependent lipid-binding-like protein, phosphatidylinositol 3-and 4-kinase, myo-inositol transmembrane transporter, phosphat-idylinositol phosphatase, inositol bisphosphate phosphatase, etc. [83]. Transcriptome and proteomic analysis of aerial and subterranean pegs in groundnut revealed expression of more than 100 HSPs-related unigenes associated with gravitropic response, mechanical stimulus and light and dark regulation. Among these, 13 HSPs were proposed to be key controllers of gravitropic response [84]. HSPs are also known to be associated with embryo abortion [85, 86]. HSP-70 is highly expressed in the aerial peg, while its expression is attenuated in the subterranean peg during swelling and pod formation [83]. Photoreceptor phytochromes play a central role in photomorphogenesis and are also likely to be involved in gravitropism. It was found that far-red and darkness can induce pod development by suppressing peg elongation, which suggests that phytochrome may control peg and pod development [75]. Further, darkness induces loss of flavonoids via reduced expression of gene chalcone synthase (CHS) a key enzyme in the flavonoid biosynthesis pathway [87], which facilitates lignin synthesis in the developing pod by diverting substrates to lignin biosynthesis. In addition, subterranean peg displays significantly reduced expression of genes encoding for brassinosteroid receptor and brassinosteroid insensitive 1-associated receptor kinase 1, with increased level of gene transcripts involved in ethylene biosynthesis which could be linked to the triple response phenotype of subterranean peg. Auxin together with BR and ethylene is known to be involved in the tripartite control of hypocotyl growth [88].

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