Journal of Agriculture and Food Research 9 (2022) 100320

Contents lists available at ScienceDirect

Journal of Agriculture and Food Research

journal homepage: www.sciencedirect.com/journal/journal-of-agriculture-and-food-research

Morphological and molecular insights of calcium in peanut pod development

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ARTICLE INFO

Keywords:
Peanut
Calcium
Pod development

ABSTRACT

Calcium is an important secondary macronutrient after nitrogen, phosphorus and potassium for the proper development of the plant. It is typically important for the formation of cell walls, cell members and accumulates in the plant cells. Calcium deficiency occurs rarely in nature but excess calcium limits plant communities on calcareous soils. In peanut, calcium uptake by plants from the soil will remain in the plant tissues and will not be transported back to developing pods where calcium requirement is more. The geotropic growth of peanut pods had capacity of absorption of calcium from the soil for filling and development of pods. Application of calcium before the pod development stage in peanut is required to have sufficient calcium available to the pods which could help an increase in yield up to 20–30%. The calcium-related genes in different metabolic pathways help in the regulation of embryo abortion in peanut and also a well-documented role in mediating plant responses to abiotic and biotic stimuli. This article provides a summary of the role of calcium, its management details, the transport of calcium into plants through the soil and overview of calcium genes in peanut pod development.

1. Introduction

Plant nutrition is an important contributing factor to plant health, for improving yield, productivity and quality of the produce. Plants being sessile in nature absorb most of their nutrients from the soil. It is reported that 95% of our food is directly or indirectly obtained from the soils [1]. In 21st century, managing soil nutrients to provide enough food supply and protect the environment are the immense challenges [2] and the essential plant nutrients would be the single most important factor limiting crop yields, particularly in developing countries. It has been estimated that 60% of cultivated soils suffer from growth-regulating problems such as deficiencies and toxicities of nutrients globally [3]. Increasing crop production and maintaining plant health is possible only by conserving the soil fertility and therefore they can transport nutrients at the right quantity and at the right time to the plants [4,5]. During 20th century, 50% of the increase in crop yields worldwide is due to the application of chemical fertilizers [6]. The cereals like wheat, rice and maize are consuming nearly 50% of all mineral fertilizers and countries like China, the USA and India are consuming about 50% of all mineral fertilizers produced in the world [7]. The mineral fertilizer usage is expected to increase from 175 million tonnes in 2015 to 199 million tonnes in 2030 in the world [8].

The soils of the semi-arid tropics (SAT) are nutritionally deficient and further accompanied by low and uneven rainfall distribution and high temperatures [9]. The SAT regions are mostly drylands with an aridity index in the range of 0.2–0.5 [10] and frequently been degraded by historical land use resulting in low soil carbon content and poor soil structure. The major threat to soils in SAT regions includes erosion, salinity and degradation due to human anthropogenic activities [7]. So, the management of nutrient status in SAT soils is of utmost importance to improve the productivity of the crop.

Peanut is an important cash crop and poor man's protein [11]. It is the 13th most important food crop in the world and the third major oilseed crop in the world. It is a low priced commodity but a treasure house of many nutrients. It contains fat (48–50%), protein (25–28%), carbohydrates (10–20%) and an excellent source of vitamins and minerals [12]. Global area and production of peanut for 2018 is reported as 28.5 million ha and 45.9 million tonnes [13]. Even though peanut is moderately drought tolerant, it suffers from nutrient deficiencies. It is an exhaustive crop and it removes a huge quantity of micronutrients and macronutrients depending on the yield [14].

Plants during their life cycle require nearly 17 essential nutrients in

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https://doi.org/10.1016/j.jafr.2022.100320
Received 4 October 2021; Accepted 14 May 2022
Available online 20 May 2022

variable amounts [15]. Depending on the function played by the nutrients in plants and their requirements they are categorized as macronutrients and micronutrients. Macronutrients are again classified as primary and secondary macronutrients. Primary macronutrients are required in the largest amount and those are carbon, hydrogen, oxygen, nitrogen, phosphorus and potassium. Out of this carbon, hydrogen and oxygen are obtained from the atmosphere directly and the rest of the nutrients are stored in the soil and are absorbed through the roots. The secondary macronutrients are needed in moderate amounts compared to primary essential nutrients and include calcium, magnesium and sulphur. Among the macronutrients, phosphorus, calcium, sulphur, potassium and magnesium are required in large quantities for peanut as these are involved in proper pod development, kernel formation and filling and oil synthesis (Singh et al., 1994).

2. Importance of calcium in peanut

Calcium is one of the important mineral elements present in the soil and plays a prominent role in many biochemical and metabolic processes (Fig. 1). Calcium is the most critical element in the development of pods and seeds and is the main limiting factor of peanut production in many parts of the world [16]. Lack of calcium reduces the yield and quality of peanut compared to any other nutrients in the soil [17]. The calcium requirement is very high particularly during the gynophore development and pod filling stage (Zharare et al., 1997).

Calcium deficiency reduces yield and quality and increases disease susceptibility, and causes poor seed germination in peanut [18,19]. Calcium deficiency influences seed development and it produces aborted seeds and unfilled pods called "pops" [20]. It also reduces the number of sound mature kernels (SMK) in the peanut. It has also been shown that deficiency decreases the seed quality by inhibiting plumule development in peanut [21,22]. [23] reported a positive correlation between the percentage of locules that filled and shelling percentage and confirmed the poor shelling percentage as an index of calcium deficiency. The presence of appropriate quantities of calcium in the soil helps to prevent black hallow, decreases aflatoxin production and decreases decayed pods and cracked pods of peanut [24]. The deficiency symptoms are development of local pitted patches on the lower surface of leaves, which eventually transforms into huge necrotic spots, indicates a calcium deficit in the leaf. Cracking of basal stem and dieback of a shoot at the later stages of growth are also reported.

3. Management of calcium in soil

Calcium (Ca) is a dominant basic cation in soils and predominant in acid soils with low CEC. Calcium source serves two functions – as a nutrient source and also as liming material to neutralize soil acidity. The major sources of liming materials are limestone (calcitic, dolomitic and hydrated), lime, slag and the major sources of calcium fertilizers are gypsum, $CaCl_2$, $Ca(NO_3)_2$, Ca-Chelates. The lime and gypsum are the commonly used calcium fertilizers and their application based on the need. Generally, lime applied at the time of ploughing and gypsum is applied at the time of flowering in peanut and it differs based on the crop. Gypsum ($CaSO_4$. $2H_2O$) contains 23.3% Ca and 18.5% Sulphur, whereas lime (Cao) contains 35.5% calcium. The application of lime changes the pH of the soil and reclaims the soil from acid to alkaline condition and the application of gypsum does not have any influence on the pH of soil. The lime alleviates aluminium toxicity in the soil whereas the gypsum reduces the availability of minerals like K and Mg. The lime has the ability to slow release of calcium due to its low solubility (0.01g/lit) in the soil and could be available up to 20 months. In contrast, the gypsum has the ability to quick-release calcium due to its high solubility (2.6g/lit) and leaching and available for only 40 days in the soil to the plants.

The critical levels of soil calcium for proper growth of a plant are about 120 ppm (0.6 meq/100 g) [25]; soil critical Ca levels is 290 kg/ha [26] but others reported as 250 ppm [27]. [28] reported that 3 meq/100 g of soil in the top 5 cm of soil surface or pod zone and 1 meq/100 g soil in the root zone are considered as threshold concentrations of calcium sufficiency in Indian conditions. The value of 1 m eq exchangeable Ca 100 g^{-1} in the root zone of soil and three times of this in the pod formation zone is reported as threshold levels for calcium content [29].

In case of peanut, higher calcium is required during pod filling than flowering, and it is more for flowering than vegetative growth [17]. The top 10 cm of soil surface also called the pegging zone is the critical area of adequate amounts of calcium for developing pods in peanut [30]. Peanuts that are runner types spread their pods more than bunch types, permitting them to extract more calcium by increasing the amount of soil available for absorption. The most essential phase for calcium supply for peanut fruit development is 15–35 days after the gynophore reaches the soil [31–33]. [33] found that most of the calcium of around 92% absorbed by the pods in 20–80 days after peg penetration into the soil out of which 69% of calcium is absorbed within 20–30 days.

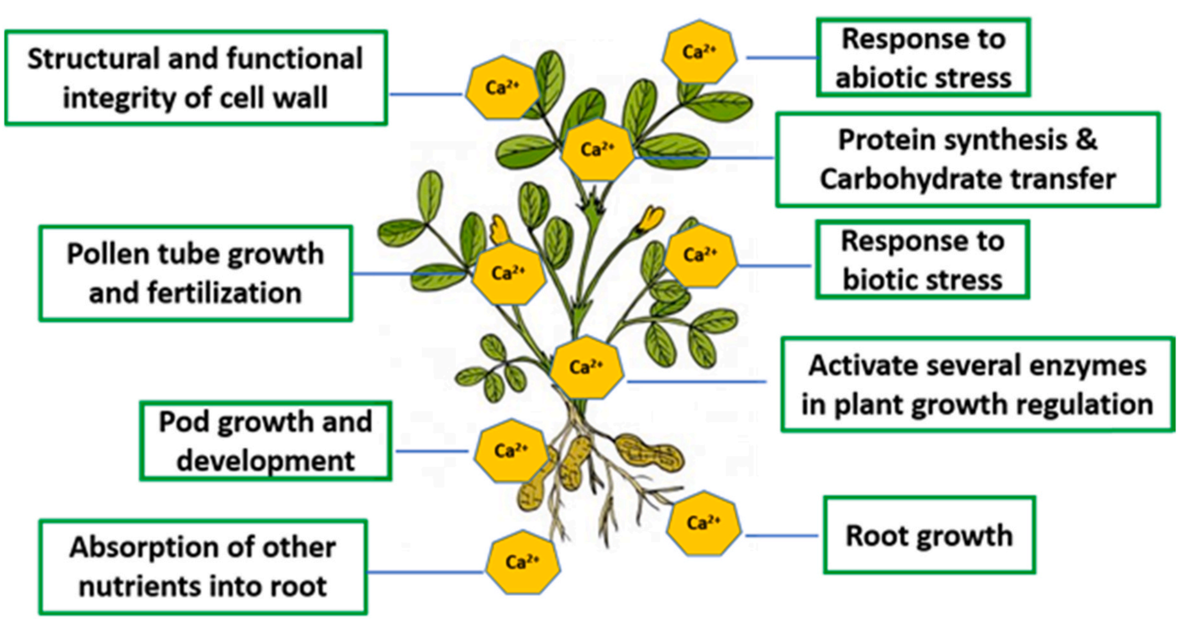

Fig. 1. Role of calcium in various developmental processes of plant.

Calcium was applied during the start of early flowering, which starts around 40 days after sowing and lasts 70–90 days, depending on the variety and climatic conditions [34].

The peanut yield responds more to gypsum application only when the amount of calcium in the soil is less than 125 mg/kg [35] and runner type cultivars respond well when residual calcium in the soil is below 225 kg/ha [36]. Incorporating lime before planting and topdressing with gypsum at flowering, corrected poor pod filling and enhanced kernel yields, according to greenhouse and field trials using calcite lime and gypsum [37].

4. Impact of calcium on peanut yield and productivity

Several workers have reported the beneficial effects of calcium on peanut [38–40]. Shallow incorporation of 1000 kg/ha limestone (90% CaCo3), before planting produced maximum yield by Virginia peanut [41]. The gypsum at the rate of 250–500 kg/ha contributed higher pod yield over the absence of gypsum application [42]. Furrow application of 2–4 q ha^{-1} calcium carbonate and gypsum to the acid soil increased pod yield of peanut to the tune of 47.6%. The improvement in crop yield is mainly due to gypsum rather than an increase in soil pH [43]. Split application of gypsum at the time of sowing and 35DAS at the rate of 500 kg ha^{-1} increased pod yield by 13.5% and dry matter production by 7.3% compared to without gypsum application [38]. A linear improvement in yield was observed when the gypsum application was increased from 200 to 500 kg ha^{-1} [44]. 500 kg gypsum fed^{-1} significantly increased the weight of pods per plant, shelling percentage and pod yield fed^{-1} [45]. According to Ref. [46] recommended dose of gypsum (400 kg ha^{-1}) significantly increased the haulm and pod yield, quality and nutrient uptake.

The calcium had optimistic effect on the shelling percentage and number of mature pods per plant [47]. The gypsum application at the rate of 500 lb/acre recorded higher peanut pod yield compared to the zero gypsum application due to the adequate availability of Ca in the fruiting zone [39]. The presence of a 7% $CaCO_3$ level in the soil produced the highest pod yield compared to 5%, 10%, 15% and 20% [48]. The application of gypsum at the rate of 0.5 and 1.0-ton gypsum fed^{-1} increased 29.5% and 20.8% hay yield, 10.1% and 22.4% pod yield, and 27.9% and 24.7% for seed yields [49]. Among four treatments (0, 125, 175, 250 kg/ha) and the application of 250 kg/ha of gypsum increased the mean pod dry weight by 39% [50]. It was evident that different growth parameters and yield of peanut were increased significantly with the application of gypsum @ 200 kg/ha (Yadav et al., 2014). The yield increased in peanut by 26.92% due to the application of 14 kg CaO and 21.65% increase due to application of 28 kg CaO [51].

The application of gypsum alone without considering soil moisture will affect peanut peg development and pod fill [52]. Drought conditions during the growth stages of peanut can reduce the number of pods, size of pods, yield and grade of seed and also causes poor seed germination [53]. The pod filling stages from R4 to R7 are the peak stages for water use and absorb nearly 0.6 cm per day and are more susceptible to moisture stress [54]. A study of the combined effect of gypsum and drought in three peanut genotypes revealed that gypsum does not influence pod initiation under sufficient irrigation but was beneficial during pod set and pod filling when water was withheld [55]. Under drought stress, applying Ca fertilizer increased pod and kernel yields which is due to an increase in the number of pods per plant and kernel rate under drought stress [56]. It was suggested that 300 kg/ha gypsum application is the best choice to lessen the impact of drought stress on peanuts [57]. The gypsum application can increase yield and SMK when calcium is below a critical level in non-irrigated soil [58].

5. Impact of calcium on quality traits of peanut

Beyond the positive role of calcium on yield enhancement, there are several other factors also influenced by calcium application. An increase in germination rate, oil content, protein content, seed calcium concentration, increase in the number of nodules, and reducing aflatoxin contamination are few other advantages linked with calcium application in peanut.

Calcium has been directly linked to seed quality through it is essential for plumule development [21,59,60]. [61] observed a percentage increase in the oil content due to the application of gypsum to soil with low calcium content. Applying gypsum (240 kg Ca ha^{-1}) during the flowering stage increases nodules/plant, protein content and oil content [62]. There is a significant increase in oil yield per hectare by increasing gypsum application from 0 to 400 kg ha^{-1} [63]. [47] found that there was an increasing trend in qualitative characteristics like the oil percentage and protein percentage with the increase in the level of application of calcium from 0 to 100 kg/ha. Calcium application increased the oil content of the peanut [64].

Some previous reports showed that gypsum application can increase calcium concentration in seeds of peanut. The calcium and sulphur concentration in pods and seeds of peanut increased by application of gypsum [65]. Calcium deficient soils lead to a reduction of seed calcium concentration in peanut and also leads to reduced germination and seedling vigour [58]. An increase in the rate of gypsum application in the peanut field directly proportional to an increase in seed calcium content [36]. But there are no perfect reports declaring that percentage increase in calcium content concerning the amount of calcium fertilizer application. So, further research is needed to see the relationship between calcium fertilizer and calcium content in peanut seeds [66]. reported that gypsum application leads to increase in germination percentage along with 40% reduction in aflatoxin contamination.

Rhizobium inoculation, a substitute for nitrogen fertilizer, usually triggers plant growth, development and yield [67]. The rhizobium forms nodules and symbiotically fixes N_2 in legumes [68]. It is host-specific and it varies from species to species and peanut rhizobia belonging to the genus *Bradyrhizobium* forms effective nodules [69,70]. Aluminium toxicity severely reduces root growth, nodulation and yield of legumes. It can be overcome by liming the soil to induce precipitation of aluminium. Prolonged liming leads to serious nutritional imbalances [71] and gypsum could be used as an alternative to lime in reducing aluminium toxicity and as a calcium supplement [26,72].

6. Ultrastructure of peanut gynophore and pod

Unlike other legumes, the peanut will produce flowers aerially and pods inside the soil. This special character of subterranean pods will absorb nutrients directly from the soil for their growth and development. After fertilization, the ovary is in the arrested stage until it reaches the soil. The elongation of gynophore takes the ovary near to the soil when the tip of gynophore reaches the soil ovule region pushed a few centimeters below the surface and starts developing pod [73]. The tip of the gynophore is the important site for cell division, cell elongation and production and distribution of various growth substances to the rest of the organ and plays a vital role in the growth and development of the organ as a whole [74].

The outgrowths on pods that play a prominent role in the absorption of calcium vary according to the development stages of a pod from R3 to R8 [75]. During the pod initiation stage (R3), the pod walls are relatively smooth without any outgrowths and in the R4 stage (beginning of seed filling stage) the pod hairs begin their growth and are unicellular like subterranean gynophore protuberances and rich in lenticels. At the R5 (seed filling) and R6 (full seed) stages the density and length of the hairs are prominent and mesh of hairs are embedded by sand grains and this stage can be seen with the unaided eye. At R7 (Seed maturing stage) the hairs degenerate and at R8 (Harvesting stage) the pod wall is completely devoid of hairs, and only hair remnants and lenticels remain. Biomass accumulation of fruit controls the hair growth during developmental stages R3 to R5 and the highest demand can be expected in R5 where seed development is most active. A microscopic cross-section of gynophore [73] revealed that it is anatomically very similar to a typical dicot stem.

The anatomical structure of the gynophore [76] revealed two distinct forms of hairs that are distributed on the gynophore during its development. The multicellular trichomes are located on aerial gynophore and root hair-like structures limited to a subterranean position. The aerial gynophore is rich in lenticels and stomata and the absence of stomata with few lenticels is noticed in the underground part of the gynophore. The density of hairs tends to be variable in response to soil water content inside the soil.

The gynophore is notable for the discrepancy between its stem-like anatomy and its root-like behaviour [77]. A ring is formed with a dozen or more vascular bundles around the center (pith) near the outer edge (cortex), in an arrangement the same as a stem. One to two layers of specialized cells in the inner cortex adjacent to the vascular bundles contain large amounts of starch grains. Together, these cells formed the starch sheath, which plays a vital role in gravity sensing in the gynophore [78].

In general, nutrients transport to various parts of the plant from roots through transpiration pull by phloem. But in peanut, the calcium transported through phloem could not be supplied back to developing pods. The reason behind this unavailability is due to the accumulation of calcium as calcium pectate in leaves and developing tissues. Ca movement in phloem tissues is very poor [79]. So, calcium is very crucial during pod development and the pods of peanut are directly absorbing calcium from the soil for its proper growth and development. The external application of calcium is very crucial in calcium-deficient soils for the complete development of pods in peanut.

7. Transportation of calcium into roots and pods

Calcium acts as an intracellular messenger in the cytosol and also cation for organic and inorganic counter anions in the vacuole [80]. It may enter through roots and reach the xylem in two ways, either the apoplast pathway (through spaces between root cells) or the symplastic pathway (cytoplasm of cells connected by plasmodesmata). The apoplastic and symplastic pathway's contributions to the transport of Ca to the xylem are unknown [81]. Calcium is generally distributed within the plant and the flow of uptake is from root surface to xylem then to shoot. The trigger for the initiation of uptake depends on Ca^{2+} concentrations in the cytosol and generates a Ca^{2+} signal (Fig. 2). The most common model explained the apoplastic movement from the epidermis of root to cortex and then to xylem if Casparian bands are not yet formed or destroyed at root tips or the place of lateral root emergence. Another possible way of calcium transport is a symplastic way and it interferes with Casparian bands. The Casparian bands are formed around endodermal cells and made up of mainly suberin and lignin. It inhibits the water and solutes movement into the xylem [82]. Generally, the suberization of endodermal walls prevents calcium influx [83] and Casparian bands also restrict calcium influx through apoplastic movement [81,84]. Up to endodermal cells, the calcium is entering in an apoplastic way and from there it reaches the cytosol of endodermis through channel proteins viz., Ca^{2+}-ATPases or Ca^{2+}/H^{+} antiporters. The channels mediating endodermal cell influx are currently unknown. The calcium entering through the interplay between both apoplastic and symplastic pathways would be enough for nutrition and also for various signaling pathways [81]. Once calcium enters into xylem through either of these pathways it would be transported to shoots and then redistributed within leaf cells [85].

The younger stages of pod take up calcium through passive diffusion from the soil for seed development and later stages of pod converts into metabolically inserted due to pod wall lignification [86]. The calcium in the soil solution may enter into gynophore and through pod walls in different pod development stages assumed to be the apoplastic pathway through diffusion. There is not much literature available regarding the transport mechanism of calcium into gynophore and pod walls [87]. explained the first indirect evidence that the gynophores have the capacity to uptake water and nutrients and proved acid reaction to litmus paper through small hairs on the gynophore [31]. also proved the absorption ability of the gynophores [88]. revealed the first evidence of nutrients absorption through gynophores. Calcium enters into seed by direct diffusion from the soil through the hull [30]. A relatively large

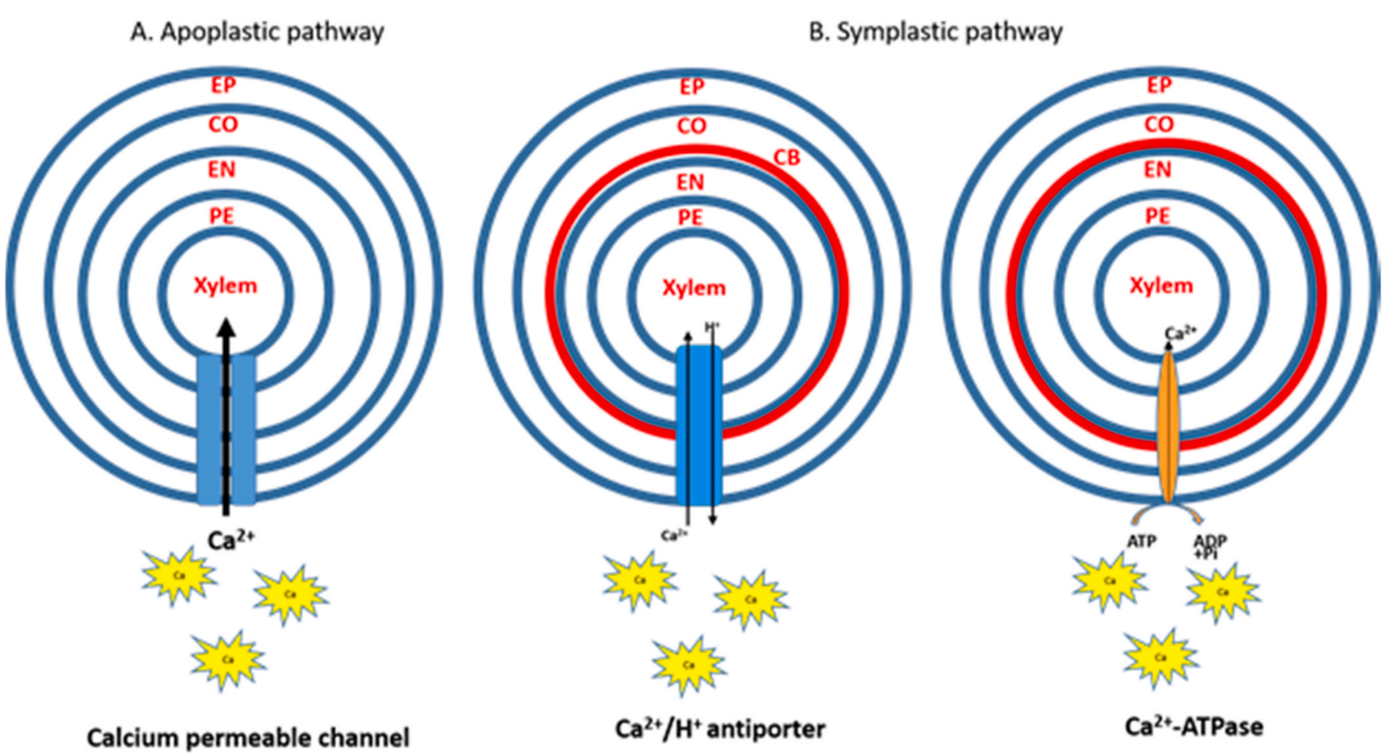

Fig. 2. Transport of calcium into the xylem of roots through different pathways.

concentration of Ca in soil solution needs to be available for uptake when pod expansion and growth is highest during growth stages R3 to R6 [75]. Microscopic analysis of peanut fruit exposed that calcium was mainly accumulated in the mesocarp and exocarp of the pod wall and outer and inner surface of the seed coat. In contrast, the seed and endocarp of the lignified pod wall recorded the lowest calcium concentration [89].

8. Molecular studies on genes and regulatory pathways involved in calcium metabolism in peanut

Calcium not only serves as an important macronutrient but also a ubiquitous hub in many enzymatic pathways. The 90% calcium available in soil was directly absorbed by peanut pods during different developmental stages of the pod [90]. Very less literature is available on the role of how calcium triggers peanut pod development after entering into the pod. As embryo development in peanut is unique and it typically geocarpic and its development is a complex process. It involves various signaling pathways and different regulatory pathways at both the transcriptional and post-transcriptional levels. To identify the perfect mechanism of calcium role inside the pods, microRNA technology is one of the best option. MicroRNAs (miRNAs) are one class of small non-coding protein RNAs which are around 18–25 nucleotides that control partial Watson Crick base-pairing regulate gene expression post-transcriptionally with their target mRNAs, leading to degradation or repression of mRNA translation (Catalanotto et al., 2014). The wide knowledge on the roles of miRNAs helps in the development of more accurate and consistent methods for examining microRNA function. A variety of conserved and novel miRNAs were identified in peanut organs like leaves, roots and stems through high-throughput sequencing technology. Few studies notified the importance of calcium in the development of pod through various pathways.

[91] studied peanut gynophores in three developmental stages (S1-aerial gynophore of 3–5 cm; S2 – 3 days after gynophore penetrated into soil; S3 – 9 days after gynophore penetrated into soil) by using 13 million short sequences and reported several enzymes which are taking part in hormone biosynthesis, signaling pathway and light signaling mechanisms and these are drastically changed during enlargement of the ovary. These genes will help in understanding the regulatory mechanisms and provide precious clues to demonstrate the mechanism of calcium signaling in the development of pod.

Proteomic analysis of different stages of gynophore of peanut was done by Ref. [92] and expressed a total of 69 proteins involved in geocarpy, 91 proteins in aerial gynophore, 35 proteins in subterranean gynophores and 26 proteins in early pods. Out of 26 proteins identified at early pod development stages involves five calcium-related genes such as calcium-binding protein, calmodulin 5, calcium-dependent protein serine/threonine kinase, endoplasmic reticulum type calcium transporting ATPase 4 and calcium-binding EF-hand family protein. This experiment indicates the role of calcium genes in the early pod development of peanut.

[93] analyzed four pod stages (1st, 5th, 10th and 20th day after peg penetration) to find out the association between Ca^{2+} excretion and pod development. Transcriptome analysis by comparing three stages identified a total of 4457 differentially expressed genes. Out of these, 53 Ca^{2+} related genes, 40 auxin-related genes, 20 ethylene related genes, 15 gibberellin genes, 7 cytokinin related genes and 2 abscisic acid-related genes are differentially expressed during different pod development stages. This study also concluded that pod development might be controlled by the collaboration of the hormonal regulatory pathways and Ca^{2+} signal transduction pathways.

Comparative transcriptome analysis of peanut gynophores and pods under Ca^{2+} sufficient and deficient conditions by Ref. [94] revealed that differentially expressed genes were found between gynophores under different regimes. During calcium sufficiency, there is an upregulation of genes related to calcium signaling pathways. This study expressed that external application calcium might help in the pod development through its signal and also promotes gynophores to other development stages. A novel miRNA analysis in the early embryo stage of peanut by Ref. [95] identified 12 specific miRNA families and 29 known and 132 potential novel miRNAs were discovered. Among them, 87 were differentially expressed during early embryo development under calcium sufficiency and starved conditions. Transcriptome analysis of peanut shells and kernels after 15 days of pegging under Ca^{2+} sufficient and deficient conditions exposed 1151 and 6423 differentially expressed genes for kernels and shells respectively. This study also revealed that shells may be more sensitive to Ca^{2+} than kernels. Genes encoding key proteins involved in nutrient absorption, ion transport, hormones, signal transduction and developmental pathways are changed significantly in this study [96].

8.1. Way forward

Although proven calcium fertilizers enhance yield in peanut, further studies also needed to evaluate the different calcium sources on various regimes of soils to identify the pathways of more calcium availability. From reviewed studies, it is clear that calcium genes play an important role directly or indirectly in pod development. But further prudent research is required to identify calcium candidate genes that are solely responsible for pod development. Furthermore, in depth analysis of characteristics of calcium genes like biological function, molecular function and cellular function and their participation in different pathways is required.

Conflict of interest

Authors declared that there is no conflict of interest to publish the article.

Declaration of competing interest

Authors declared that there is no conflict of interest to publish the article. We declare that this manuscript is original, has not been published before and not in currently being considered for publication elsewhere.

Acknowledgement

This research was supported by Science and Engineering Research Board (SERB), Government of India.

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