



RESEARCH ARTICLE

Effects of plant growth regulators on peg and pod development in peanut (*Arachis hypogaea* L.) under drought stress

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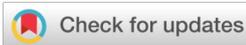
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Abstract

Peanut is a globally important legume crop consumed in various forms due to its high nutritional value. However, peanut production faces challenges, particularly under drought conditions, resulting in reduced flowering, peg and pod formation. This study aimed to investigate the changes in morphology, anatomy and activity of plant growth regulators during flowering, peg development and pod formation in peanuts, using the VD01-2 cultivar. The objective of the study was to explore the application of plant growth regulators to optimize flowering, peg development and increase pod yield in peanuts. The peanuts were cultivated at the Ho Chi Minh City High-Tech Agriculture Park under the following conditions: 150 ± 20 Klux light intensity, 45/26 ± 2 °C temperature and 35/80 ± 5 % humidity. The experimental soil composition was 63.4 % sand, 28.5 % silt and 8.1 % clay, with 24.91 g kg⁻¹ organic matter, 0.165 % total nitrogen, 0.062 % phosphorus and 0.93 % potassium. Statistical analysis of the data revealed an increase in auxin and gibberellin activity during flowering, which contributed to peg elongation. However, as the peg entered the soil and formed the pod, the activity of these plant growth regulators decreased. Additionally, the combination of 50 mg L⁻¹ IAA (indole-3-acetic acid) and 150 mg L⁻¹ GA3 (gibberellic acid) effectively enhanced the development of flowers, pegs and pods in peanut plants under drought-stress conditions. Furthermore, this combined treatment resulted in an increase in the lipid content of the seeds from 545.2 mg to 570.0 mg/g of weight. These findings have the potential to improve peanut productivity under drought conditions, addressing the challenges faced in peanut production.

Keywords

Arachis hypogaea L.; drought stress; peanuts; peg; plant growth regulators

Introduction

Peanut, scientifically known as *Arachis hypogaea* L., is a vital leguminous crop that holds significant importance in global agriculture and food production. It is widely consumed in various forms and is recognized for its high nutritional value. Peanut seeds are rich in lipids (40-60 %), proteins (25-30 %), vitamins (vitamin E, B, PP) and minerals (Ca, Fe, K), making them a valuable source of sustenance (1). They are extensively used in popular food products such as confectionery, peanut butter and animal feed. Peanut cultivation has witnessed a substantial increase, with global production reaching an impressive total of 43982066 metric tons, with Asia and Africa being the primary contributors to this remarkable output (2).

To meet the ever-growing demand for peanuts, efforts have been

made to enhance their yield, particularly by increasing the number of pods (3). However, peanut plants are highly susceptible to the adverse effects of drought stress, which can significantly impede flower production, consequently leading to a reduction in pegs (immature pods) and mature pods (4). The intricate process of flower initiation and subsequent peg and pod development is intricately regulated by various plant growth regulators (5). These plant growth regulators, including hormones such as auxins, cytokinins, gibberellins and abscisic acid, play pivotal roles in controlling plant growth, development and response to environmental cues (6). Given the significance of plant growth regulators in regulating flowering and reproductive development, investigating the changes in plant growth regulators in response to drought stress and their correlation with morphological alterations holds immense promise for enhancing peanut productivity. By studying the dynamics of plant growth regulators and their effects on peg and pod development under water-limited conditions, valuable insights can be gained to develop effective strategies for optimizing peanut yield.

The main objective of this study is to investigate the effects of plant growth regulators on peg and pod development in peanut plants subjected to drought stress. Through a comprehensive analysis of the alterations in plant growth regulators and their relationship with morphological changes, the study aims to identify and evaluate suitable plant growth regulator treatments that can ameliorate the negative impacts of drought stress on peanut crops (7). The ultimate goal is to develop practical approaches to enhance peanut yield and resilience in water-limited environments.

Materials and Methods

Plant material

Seeds of peanut (*Arachis hypogaea* L.) cv. VD01-2, procured from the Research Institute of Oil and Oil Plants in Ho Chi Minh City, Vietnam, served as the experimental material. These seeds were sown in pots at the experimental farm of the Agricultural High-Tech Business Incubation, situated within the Ho Chi Minh City High-Tech Agriculture Park. The experiment was conducted from February to May 2022. The environmental conditions at this location included an average daily light intensity of 150 ± 20 Klux, with day/night temperatures averaging $45/26 \pm 2$ °C and day/night air humidity of $35/80 \pm 5$ %. The experimental soil in the pots exhibited a composition comprising 63.4 % sand, 28.5 % silt and 8.1 % clay. Notably, the soil boasted an organic matter content of 24.91 g kg⁻¹, a total nitrogen % of 0.165 %, available phosphorus of 0.062 % and available potassium of 0.93 %. Furthermore, the soil harbored micronutrients, including 733 mg kg⁻¹ of zinc, 98 mg kg⁻¹ of boron, 26 mg kg⁻¹ of copper and 0.9 mg kg⁻¹ of molybdenum. Temporal changes in peanut morphology and anatomy were observed to discern the various developmental stages. Axillary buds, flowers, pegs and pods at their respective stages were carefully acquired and subsequently utilized for the analysis of plant growth regulator activity.

Anatomical observations

A free-hand sectioning technique was utilized to investigate the structure of peg tips. The peg tip slices were cleaned with a 5 % NaClO solution for a duration of 15 min, followed by rinsing them three times with distilled water (8). The sections were treated with a 5 % acetic acid solution for 5 min and rinsed with water 3 times. After that, the carmine-iodine dye was applied to the sections for 3 min and subsequently washed until all the excess stain was removed. Finally, slices were observed under a light microscope (CKX41, Olympus, Japan). Pod slices were placed in water on a glass slide and covered with a coverslip. High-quality images were captured using a laser scanning confocal microscope (LSCM, Leica SP2 AOBs, Mannheim, Germany) to observe anatomical changes in pods.

Determination of plant growth regulators activity

The sample was processed to extract plant growth regulators (including auxin, cytokinin, gibberellin and abscisic acid) using methanol. Thin-layer chromatography was performed using a silica gel plate and a mobile phase containing isopropanol, ammonium hydroxide and water. The chromatogram was visualized under UV light and the bands corresponding to the growth regulators were isolated. The isolated bands were scraped off and immersed in a solvent mixture of methanol, chloroform and acetic acid. The supernatant obtained after centrifugation was collected and evaporated. The resulting preparation was dissolved in water (9, 10). Different bioassays were conducted to determine the activity of each plant growth regulator (11). A rice coleoptile bioassay was utilized to measure auxin and abscisic acid levels. The difference in coleoptile length compared to the control (1 mg L⁻¹ IAA and 1 mg L⁻¹ ABA). The cytokinin activity was found to be directly proportional to the difference in fresh weight of the cucumber cotyledon as compared to the control (1 mg L⁻¹ zeatin). The level of gibberellin activity exhibited a proportionate increase in the shoot length compared to the control group (10 mg L⁻¹ GA3).

Effects of plant growth regulators on peg and pod development under drought stress

Peanut seeds were sown in pots (30 cm in height and 40 cm in width) containing soil at 75 % of field capacity (control) and 60 % (drought stress) and placed in an experimental garden. After 25 days of planting peanuts (vegetative stage, preparing for flowering), plant growth regulators were sprayed on leaves (12). These included 50 mg L⁻¹ IAA, 150 mg L⁻¹ GA3, 50 mg L⁻¹ IAA and 150 mg L⁻¹ GA3. Observe the growth of peanuts over time. Document agricultural parameters such as the number of pegs, pods and seeds as well as seed weight. Additionally, record quality-related parameters of the seeds.

Determination of the soluble sugar, starch, protein and lipid

In order to ascertain the concentration of soluble sugars, the previously described procedure was followed (13). The presence of starch was determined through the utilization of the Miller technique (14). We employed Bradford's description to determine the protein content (15). The lipid content was also extracted using an organic solvent (16).

Statistical analysis

The experiment included 5 treatment conditions and was conducted 3 times in a randomized block design, with the data analyzed using ANOVA. To separate the means at a 5 % probability level, Duncan's Multiple Range Test was employed in SPSS 20.0. The result was presented as the mean with a standard deviation.

Results

Morphological and anatomical changes of peg and pod in development stages

The reproductive stages are determined by observing visible events or microscopic changes of shoot apical meristem (R0), such as flowering, pegging, pod growth, seed growth and maturity. The beginning of bloom stage, or the R1 stage, is identified when at least 50 % of the plants have produced an open flower. After fertilization, the flower's ovary develops into a small, elongated structure called the peg (Fig. 1A). The R2 stage, or the beginning peg stage, is recognized when half plants have an elongated peg without soil penetration (Fig. 1B). The R3 stage, or the elongation peg stage, is recognized when half of the plants' elongated peg reaches its maximum length of about 10 cm (Fig. 1C). The beginning of pod stage, or R4 stage, is achieved when half of the plants have an elongated peg with an ovary tip that has begun to swell, marking the globular embryo stage (Fig. 1D & 2A). The R5 stage, or full pod stage, is achieved when the embryos have reached the late globular stage (Fig. 1E & 2B). The R6 stage, or beginning of seed stage, is distinguished when at least 50 % of the plants have pods with cotyledons that are large enough to be seen when cut with a razor blade. At this stage, the seeds were passing the liquid endosperm phase (Fig. 1F). The R7 stage, or full seed stage, is attained when half of the plants have pods with cotyledons occupying the entire endosperm cavity (Fig. 1G & 2C). The beginning of maturity seed stage, or R8 stage, is reached when 50 % of the plants have pods, where the seeds appear to fill the pod cavity (Fig. 1H). Finally, the maturity seed stage, or R9 stage, is identified when at least 50 % of the plants have pods exhibiting inner pericarp coloration (Fig. 1I).

Interestingly, the peanut plant's reproductive process involves a crucial role played by its gynophore. Following fertilization, the gynophore descends and carries the nascent seeds into the soil. While the embryos within the ovules and ovary remain dormant in the air, the peanut fruit initiates its growth once the gynophore's tip contacts the soil and pushes the ovule region underground. The tip then bends laterally and parallel to the soil, resulting in the characteristic form of the peanut pod. Moreover, the peanut gynophore has distinctive anatomical and morphological traits. During the R2 stage, most cell division in the gynophore takes place in the distal region, roughly 2-5 mm from the tip. This part of the gynophore is recognized as an intercalary meristem, situated between sections of differentiated vascular bundles and mature tissue (gynophore) (Fig. 3A). As the peg reaches its maximum length in the R3 stage, the intercalary meristem in the tip disappears (Fig. 3B). The peg then undergoes geotropic growth, causing the region with the embryo to be buried underground in the R4 stage. During this stage, cell division of the gynophore resumes in the darkness, forming the epicarp and mesocarp (Fig. 3C).

Changes of plant growth regulators activity in peg and pod development

Based on the data in Fig. 4, the analysis reveals specific patterns in the activity of different plant growth regulators during the process of flowering, peg development and pod formation in peanuts. Auxin activity showed an increase during the flowering phase, from the R0 stage to the R1 stage (0.11 to 0.36 mg L⁻¹). This increase remained consistent and contributed to peg elongation, which occurred from the R1 to R3 stages. However, once the peg entered the soil (R4 stage) and started to develop into a pod (R5 stage), the auxin activity decreased (from 0.36 to 0.25 mg L⁻¹). Similarly, the activity of gibberellin followed a similar pattern to auxin. It exhibited a significant increase during flowering and peg elongation (R1 to R3 stages) and then decreased as the peg entered the soil and formed the pod (R4 and R5 stages). In contrast, cytokinin activity remains relatively unchanged from the beginning bloom stage until peg elongation. It is only when the tip of the peg has entered the soil and began to grow and form the pod that cytokinin activity increases (from 0.15 to 0.27 mg L⁻¹). The activity of abscisic acid (ABA), on the other hand, did not show significant changes throughout the entire process of peg and pod development. It remained relatively consistent and did not exhibit any distinct patterns of increase or decrease.

Effects of plant growth regulators on peg and pod development under drought stress

The statistical analysis indicated that the application of 50 mg L⁻¹ IAA resulted in a significant increase in the number of flowers, pegs, pods and seeds compared to plants subjected to drought stress alone. However, the effect observed with the 150 mg L⁻¹ GA3 treatment was even greater. Notably, when a combination of IAA and GA3 was applied, there was a synergistic effect, leading to a higher number of pegs, pods and seeds compared to the control group. Specifically, the combination of IAA and GA3 increased the number of flowers from 14.8 to 66.6, resulting in an approximate increase of 30 pegs and 17 pods. Moreover, the concurrent application of IAA and GA3 resulted in a noteworthy reduction in the starch, total sugar and protein content within the seeds. Conversely, this treatment notably amplified the lipid content within the seeds, culminating in a measure of 570.0 mg, as opposed to the control group's 489.2 mg (Table 1). This holds significance as the lipid content stands as the principal nutritional constituent in seeds.

Discussion

The changes in plant growth regulator activity observed during flower, peg and pod development stages in peanuts have significant implications for the morphological and anatomical transformations. Auxin, a key plant growth regulator involved in plant growth and development, shows increased activity during the beginning bloom stage (from R0 to R1 stage) and remains consistently high as the peg elongates in the R2 and R3 stages (Fig. 4). During the R2 stage, cell division mainly occurs in the distal region of the gynophore, known as the intercalary meristem (Fig. 3A). This region is situated between sections of differentiated vascular bundles and mature tissue. As the peg reaches its maximum length in the R3 stage, the

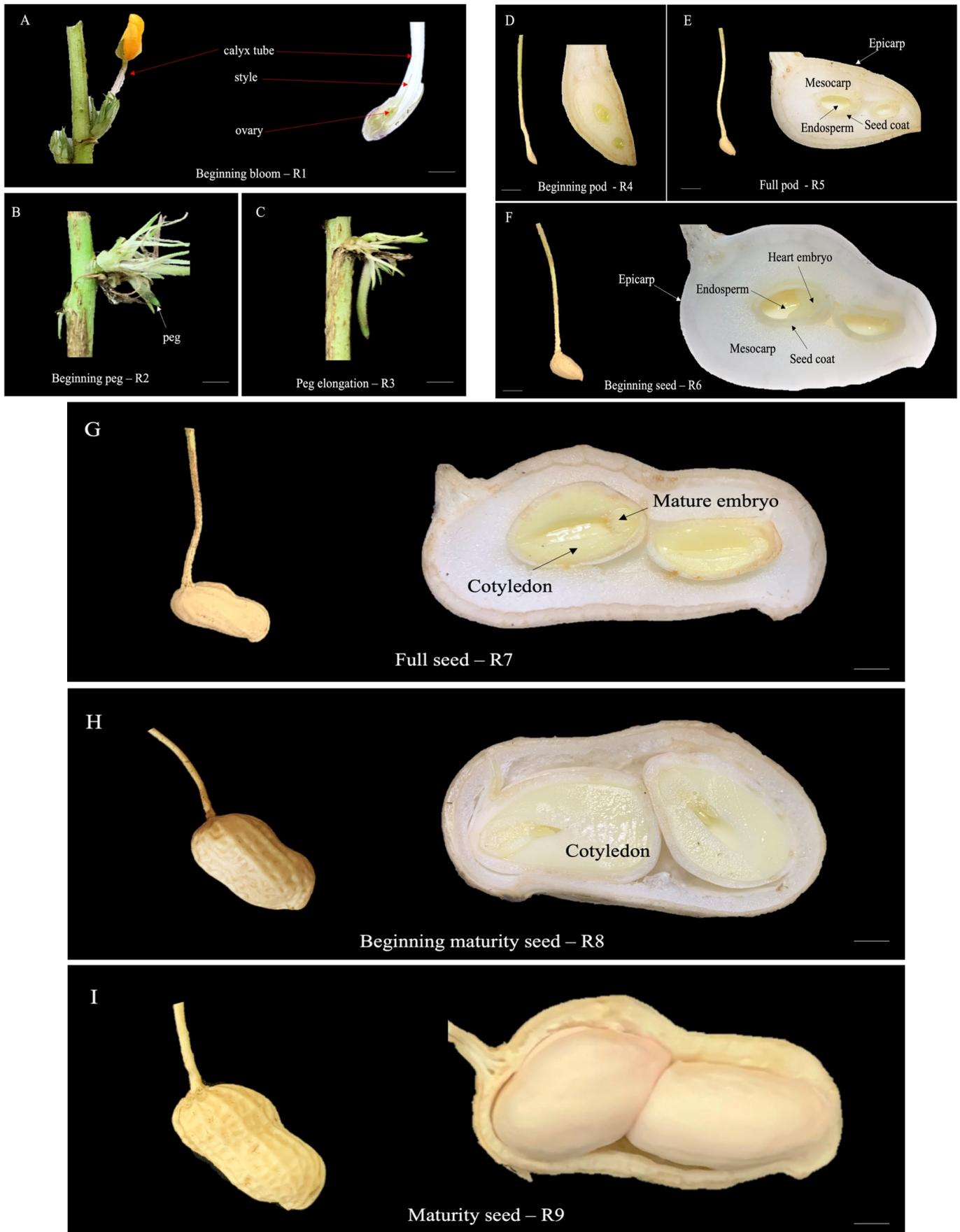


Fig. 1. The development stages of peg and pod in peanut. Scale bar = 1 cm. A. Flower in the beginning bloom stage (R1); B. Emasculated ovary at the base of gynophore and emergence of peg in the beginning peg (R2); C. Peg elongation and bending towards gravity in the peg elongation stage (R3). (D) The development stages of peg and pod in peanut. Scale bar = 1 cm. Peg penetration into the soil (R4); E. Pod growth consists of distinct parts: the shell, the seed coat, the endosperm and the late globular embryo. The shell comprises 2 parts, with the outer layer being lignified (epicarp) and the inner layer being mesocarp. The seed coat is a thin layer of cells that surrounds the kernel in the full pod stage (R5). (E) The development stages of peg and pod in peanut. Scale bar = 1 cm. F. Cotyledons are visible and the liquid endosperm phase is nearly complete in the beginning seed stage (R6); G. Cotyledons fill the entire endosperm cavity in the full seed stage (R7); H. Seeds appear to fill the pod cavity in the beginning maturity seed stage (R8); I. The pericarp interior with coloration in the maturity seed stage (R9).

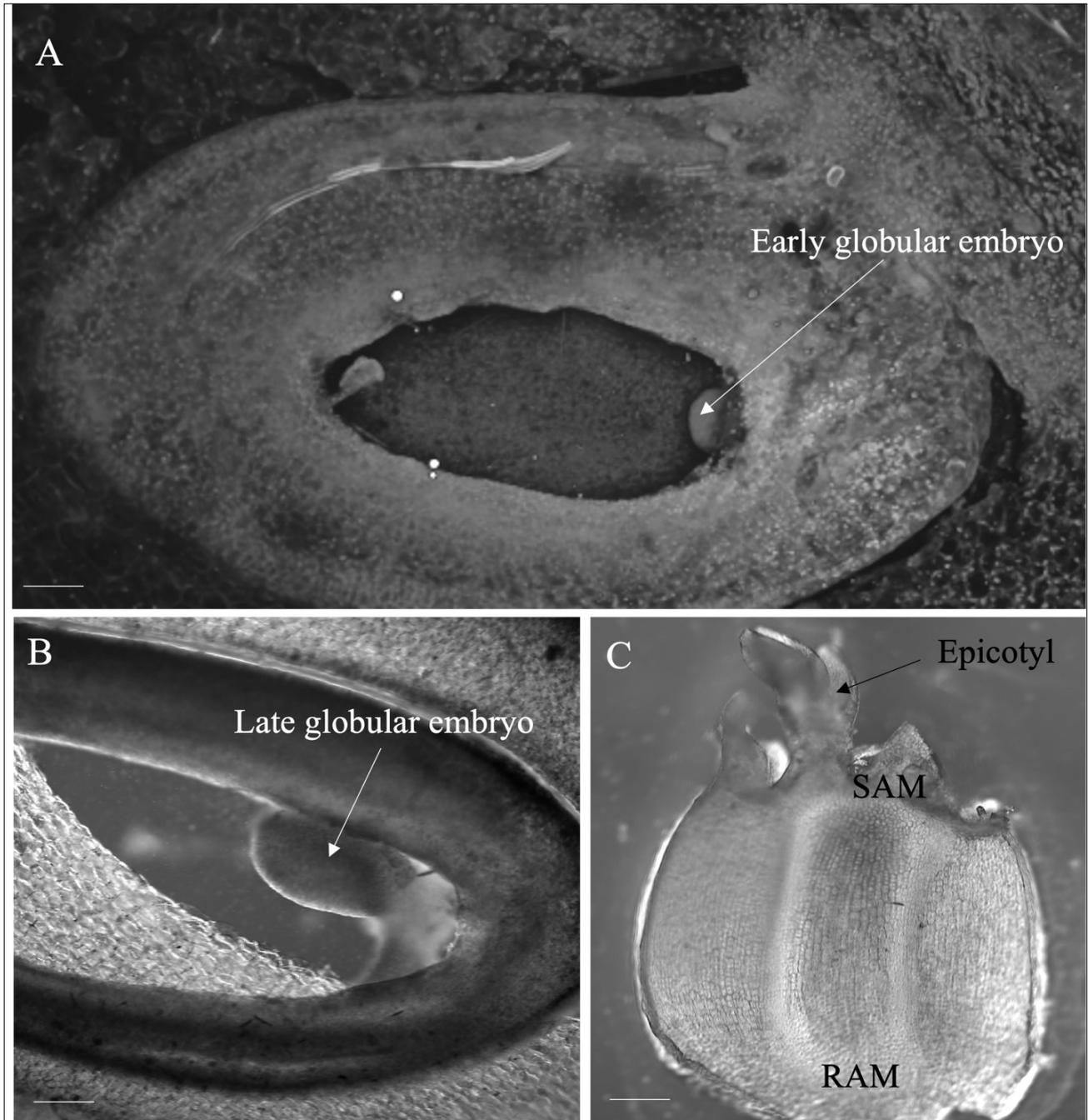


Fig. 2. The development stages of embryo. Scale bar = 0.5 mm. **A.** The early globular embryos in the R4 stage; **B.** The late globular embryo in the R5 stage. **C.** The mature embryo with epicotyl, shoot apical meristem (SAM) and root apical meristem (RAM) in the R7 stage.

Table 1. Effects of plant growth regulators on the number of flowers, pod and seed number, seed weight and contents of lipid, starch, sugar and protein in peanut seed at harvest time under drought stress

Parameters	Treatment				
	Control	Drought	IAA 50 mg L ⁻¹	GA ₃ 150 mg L ⁻¹	IAA 50 + GA ₃ 150 mg L ⁻¹
Flower number	66.4 ± 0.9 ^a	14.8 ± 1.6 ^d	33.2 ± 0.5 ^c	59.2 ± 6.6 ^b	66.6 ± 7.4 ^a
Peg number	33.2 ± 2.1 ^{ab}	5.6 ± 1.1 ^d	17.6 ± 0.2 ^c	31.4 ± 3.5 ^b	35.3 ± 3.9 ^a
Pod number	16.2 ± 1.3 ^b	2.6 ± 0.6 ^d	9.0 ± 0.1 ^c	16.0 ± 1.8 ^b	19.1 ± 2.1 ^a
Seed number	30.3 ± 3.2 ^b	5.2 ± 1.1 ^d	17.9 ± 0.2 ^c	32.1 ± 3.6 ^b	38.1 ± 4.2 ^a
Seed weight (g)	0.6 ± 0.0 ^a	0.5 ± 0.0 ^b	0.5 ± 0.0 ^b	0.6 ± 0.0 ^a	0.6 ± 0.0 ^a
Lipid (mg/g)	489.2 ± 10.4 ^d	545.2 ± 16.1 ^{bc}	559.2 ± 16.6 ^{ab}	527.6 ± 4.3 ^c	570.0 ± 18.7 ^a
Starch (mg/g)	65.7 ± 3.6 ^a	41.9 ± 2.6 ^b	42.6 ± 1.8 ^b	34.8 ± 2.1 ^c	34.6 ± 3.9 ^c
Sugar (mg/g)	44.5 ± 1.7 ^c	47.7 ± 2.5 ^b	44.3 ± 1.4 ^c	61.7 ± 3.1 ^a	35.2 ± 2.6 ^d
Protein (mg/g)	267.9 ± 8.9 ^b	296.3 ± 8.9 ^a	269.4 ± 11.9 ^b	294.4 ± 4.9 ^a	253.6 ± 13.8 ^c

Values with different letters in a row are significantly different according to Duncan's test ($p=0.05$)

intercalary meristem disappears (Fig. 3B). It can be inferred that the presence of auxin essentially facilitates the growth of pegs. The high auxin levels during these stages likely stimulate cell division and expansion, contributing to the elongation of the peg. However, the auxin activity decreases once the peg penetrates the soil (R4 stage) and forms a pod (R5 stage) (Fig. 4). This decrease in auxin activity may be associated with the transition from peg elongation to pod development. Gibberellin exhibits a similar pattern of activity to auxin during peg development. It increases significantly during peg elongation and decreases as the peg enters the soil (Fig. 4). The role of gibberellin in peg elongation is consistent with its well-known function in promoting cell elongation (5). The decline in gibberellin activity as the peg penetrates the soil suggests that other factors become more critical for subsequent pod development. Cytokinin, a plant growth regulator involved in cell division and differentiation, shows relatively stable activity from the beginning bloom stage until peg elongation (17). Its activity increases when the tip of the peg enters the soil and starts to grow, forming the pod (R4 and R5 stages) (Fig. 4). During these stages, cell division resumes in the darkness, forming the epicarp and mesocarp (Fig. 1). It is strongly suggested that cytokinin is pivotal in promoting cell division and differentiation in pod development. The timing of cytokinin activity coincides with the resumption of cell division in the gynophore, leading to the formation of the epicarp and mesocarp. In contrast to auxin, gibberellin and cytokinin, abscisic acid does not exhibit significant changes in activity throughout the entire process of peg and pod development (Fig. 4). ABA is known for its involvement in seed dormancy and stress responses rather than active growth processes (18). Moreover, the activity of ABA is not only dependent on its concentration but is also influenced by the coordinated effects of other plant growth regulators, particularly auxin. According to some researchers, auxin and ABA share common signaling components, such as the ubiquitin-proteasome system, which regulates the degradation of transcriptional repressors (19). Crosstalk between auxin and ABA pathways occurs at the level of transcriptional regulation, where they can influence each other's target genes. Auxin can inhibit ABA biosynthesis, leading to a reduction in the impact of ABA in plants. This helps explain why the activity of ABA during most stages of fruit development does not undergo significant changes. Based on

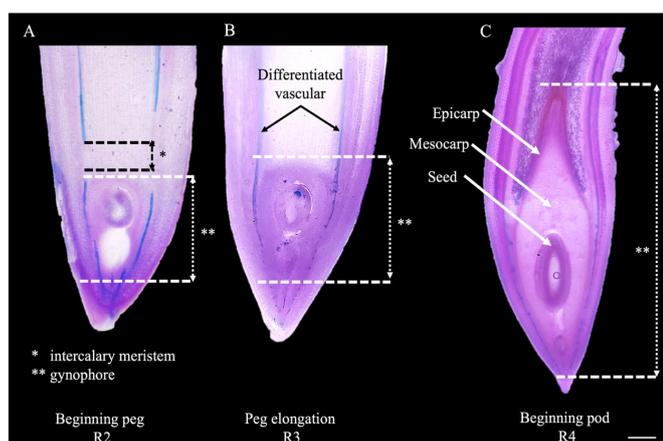


Fig. 3. Anatomical analysis of peanut pegs from R2 to R4 developmental stages. Scale bar = 1 mm. (A) beginning peg stage - R2; (B) peg elongation stage - R3; (C) beginning pod stage - R4.

the available data, it appears that auxin and gibberellin exert a significant influence on flower, peg formation and elongation, while cytokinin likely plays a role in pod development and differentiation. These findings suggest that the interplay between these plant hormones is a key factor in determining the growth and development of peg and pod and may have important implications for agricultural productivity.

The application of plant growth regulators, specifically IAA and GA3, has demonstrated efficacy in ameliorating the adverse effects of drought stress and enhancing the development of pegs and pods, as presented in Table 1 and Fig. 5. Multiple studies across various plant species have consistently reported favorable outcomes from the application of IAA and GA3 in augmenting pod yield and quality under diverse stress conditions. Notably, in mungbean, the combined treatment of IAA and GA3 resulted in an increased pod yield through the promotion of flowering and fruit set, as well as improvements in seed quality, including elevated total carbohydrate and protein content (20). In the present study, the combined application of IAA and GA3 did not increase the levels of starch, total sugar, or protein in peanut plants. However, a significant rise in lipid content was observed. According to some researchers, the peanut plant's natural inclination to store lipids as its primary seed constituent is a genetic trait (21). Consequently, the concurrent use of IAA and GA3 leads to the redirection of total sugars in the plant towards lipid synthesis, thereby diminishing the allocation of resources to protein and starch production. This phenomenon ultimately leads to a reduction in other storage constituents such as protein, starch, and total sugars. The utilization of IAA and GA3 holds promise for enhancing plant growth and development by facilitating processes such as cell division, elongation and differentiation. IAA, primarily accountable for promoting cell elongation, modulates the activity of cell wall loosening enzymes, thereby enabling cellular expansion and elongation (22). Synthesized in the apical meristems of plants, IAA is transported downward towards elongating tissues (23), contributing to the overall growth of stems and pegs in peanuts. Conversely, GA3 plays a role in stem elongation and branching, stimulating cell division and elongation in the internodal regions of stems (24). Additionally, this hormone influences the development of lateral buds, thereby promoting

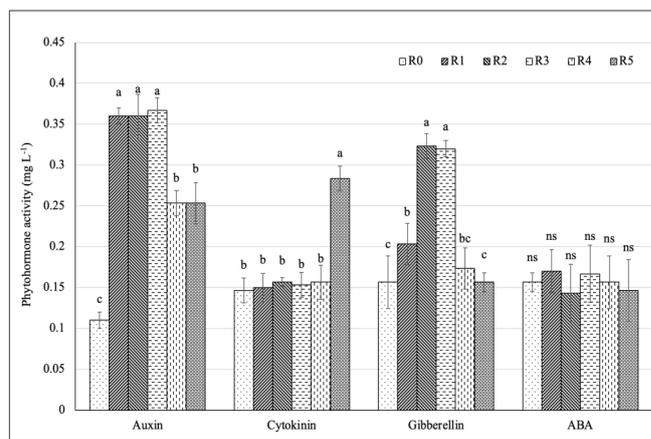


Fig. 4. Changes of plant growth regulators activity in peg and pod development (R0 - vegetative stage; R1 - beginning bloom; R2 - beginning peg stage; R3 - elongation peg stage; R4 - beginning pod stage; R5 - full pod stage). Values with different letters in a column are significantly different according to Duncan's test ($p=0.05$).

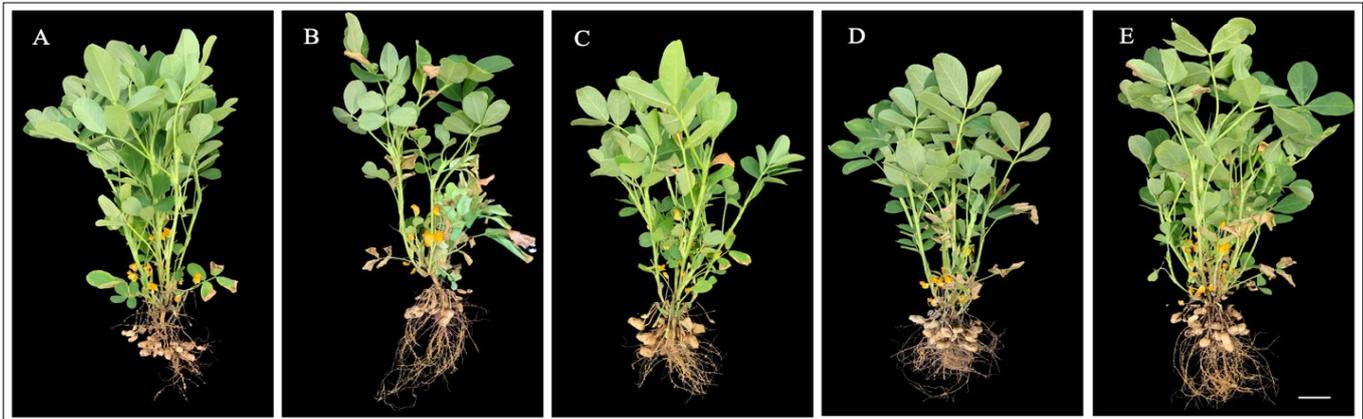


Fig. 5. Effect of plant growth regulators on peg and pod development under drought stress. Scale bar = 5 cm. (A) control; (B) drought stress (C) 50 mg L⁻¹ IAA; (D) 150 mg L⁻¹ GA₃; (E) 50 mg L⁻¹ IAA and 150 mg L⁻¹ GA₃.

flowering, branching and the generation of new shoots (25). The novelty of the current study lies in its focus on understanding the effects of IAA and GA₃ application on peanut, a major legume crop, under drought stress conditions. The comprehensive analysis of plant growth regulator alterations and their relationship with morphological changes provides valuable insights into the mechanistic basis of how these phytohormones can ameliorate the negative impacts of drought on peanut peg and pod development. The findings of this study have important implications for the development of practical approaches to enhance peanut yield and resilience in water-limited environments. Future research could explore the interactions between plant growth regulators and other environmental factors, such as soil nutrient status and temperature, to further optimize the application of these phytohormones. Additionally, screening and development of peanut cultivars with improved drought tolerance, in combination with targeted plant growth regulator treatments, could be a promising avenue to enhance the productivity and sustainability of peanut production under drought-prone conditions.

Conclusion

The reproductive stages were determined by visible events and microscopic changes, including flowering, pegging, pod growth, seed growth and maturity. In there, auxin and gibberellin activity exhibit a similar pattern, with an increase during the early stages of flowering, peg development and a subsequent decrease as the peg enters the soil and forms the pod. In contrast, cytokinin activity remained stable during peg elongation and increased during pod formation. Applying a combination of 50 mg L⁻¹ IAA and 150 mg L⁻¹ GA₃ has shown promising results in enhancing the development of flowers, pegs and pods, even under drought-stress conditions. This combined treatment increased the number of flowers, pegs, pods and seeds and resulted in a higher lipid content in the seeds. Building on these findings, future research should explore the optimization of the hormone application rates, timings and methods to further maximize the beneficial effects on peanut growth and yield. Investigating the interaction between these plant hormones and other environmental factors, such as water availability and nutrient status, could also yield important insights to develop more robust and resilient peanut cultivation practices.

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Authors' contributions

TTT carried out the experiments and drafted the manuscript. HTT and VBT conceived of the study and participated in manuscript editing, its design and coordination. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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