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Evaluation of Molecular and Agronomic Responses of Peanut under Different Cultivation Conditions

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Abstract Peanut (*Arachis hypogaea* L.) is an important oilseed and economic crop, and its growth, yield formation, and quality are strongly influenced by cultivation conditions. This review summarizes the effects of different cultivation practices, including planting density, water management, and nutrient regulation, on peanut agronomic traits, physiological processes, and molecular responses. The mechanisms underlying photosynthetic regulation, root system adaptation, stress defense, and metabolic adjustment under diverse environmental conditions are discussed. Furthermore, advances in molecular approaches, including transcriptomics, metabolomics, proteomics, and integrated multi-omics analysis, are highlighted to elucidate the regulatory networks involved in peanut environmental adaptation. A comprehensive evaluation framework combining phenotypic traits, physiological indicators, molecular responses, and predictive modeling is proposed. A case study focusing on water and fertilizer management demonstrates the interactions between cultivation practices, agronomic performance, and molecular regulation. Future perspectives emphasize the integration of precision agriculture, molecular breeding, and intelligent management strategies to improve resource-use efficiency, stress resilience, and sustainable peanut production.

Keywords Peanut; Cultivation conditions; Agronomic traits; Molecular regulation; Precision agriculture

1 Introduction

Peanut (*Arachis hypogaea* L.) is a globally important oilseed and food legume that supplies edible oil, protein, and other nutrients, and it contributes directly to food and nutritional security in many tropical and subtropical production systems (Puppala et al., 2023). It is cultivated widely across developing regions and more than 100 countries, where it serves as a principal source of digestible protein, cooking oil, and vitamins, especially in areas facing persistent malnutrition and resource limitation. Peanut also has broader agronomic value because it improves soil fertility through biological nitrogen fixation, while its seeds contain diverse bioactive compounds that enhance its nutritional and economic importance. However, the environments in which peanut is grown are becoming increasingly unstable. A large proportion of production occurs in arid, semi-arid, or otherwise suboptimal environments, where drought, heat, salinity, nutrient deficiency, and erratic rainfall patterns constrain both productivity and quality (Zhong et al., 2023; Pokhrel et al., 2025). Among these factors, drought is consistently identified as one of the most severe constraints on peanut production, particularly during reproductive and pod formation stages, when water deficit sharply reduces pod yield and kernel quality. Heat stress frequently co-occurs with drought and further amplifies damage, with reproductive-stage plants being especially vulnerable to combined stress effects that depress yield and nutritional quality. Environmental stress also raises important food safety concerns, because drought-stressed peanuts are more prone to pre-harvest aflatoxin contamination, which threatens human and animal health and reduces marketability and trade value. In addition to water and temperature stress, soil nutrient imbalance remains a major limitation under changing cultivation conditions; peanut performs better under suitable soil nutrition, yet phosphorus deficiency is widespread in peanut-growing soils and inhibits growth, yield formation, and quality-related biochemical processes. These challenges are further complicated by strong genotype-by-environment interactions, which make stress tolerance difficult to assess consistently across locations and often cause cultivars classified as tolerant in one environment to perform poorly in another.

In response to these constraints, substantial progress has been made in the study of peanut agronomic traits and molecular regulation, especially through the integration of physiology, genomics, transcriptomics, proteomics, and functional genetics. Physiological studies have shown that drought-tolerant genotypes maintain more favorable water status, antioxidant capacity, stomatal regulation, and osmotic adjustment than sensitive lines, linking agronomic performance under stress to measurable plant traits such as water content, chlorophyll retention, hydraulic behavior, and root growth. Root system architecture has emerged as a particularly important trait because deeper or more efficient root systems can improve water and nutrient acquisition under climate-related stress, although underground phenotyping remains technically difficult and labor intensive (Gelaye et al., 2025). At the molecular level, transcriptome studies have greatly expanded current understanding of peanut stress responses. Severe drought induces thousands of differentially expressed genes and highlights regulatory pathways involving MAPK signaling, flavonoid and phenylpropanoid biosynthesis, starch and sucrose metabolism, glutathione metabolism, and plant hormone signal transduction. Comparative analyses across tolerant and susceptible genotypes further show that stress adaptation depends on transcriptional stability and differential activation of signaling, reactive oxygen species scavenging, and osmotic protection pathways (Jiang et al., 2020). Similar progress has been made beyond drought alone. Under phosphorus deficiency, integrated phenotype-transcriptome-metabolome analyses identified coordinated changes in transporter genes, hormone-related genes, antioxidant systems, miRNAs, and metabolite accumulation, demonstrating that cultivation conditions reshape peanut performance through multilayer regulation rather than through isolated pathways. Genome-wide studies have also identified stress-responsive regulatory gene families, including WRKY, TGA, GASA, NCED, and Di19 members, many of which show drought- or hormone-inducible expression patterns and provide candidates for functional improvement of stress tolerance. Functional validation is increasingly moving from correlation to mechanism: overexpression of regulatory genes such as AtHDG11 and AhLEA2 has improved drought tolerance, antioxidant protection, water-use efficiency, root development, and even stress-period yield in transgenic systems, confirming that molecular candidates can have agronomic consequences. Meanwhile, advances in genome sequencing, marker development, marker-assisted selection, genomic selection, and CRISPR-based editing are creating new opportunities to connect gene discovery with precision breeding for yield, oil quality, and resilience (Umer et al., 2025).

Despite this progress, a major research need remains: peanut improvement under different cultivation conditions requires a more explicit integration of molecular responses with agronomic performance across realistic environments. Current evidence shows that stress tolerance is polygenic, environmentally sensitive, and difficult to phenotype accurately in field settings, where soil heterogeneity, moisture variation, and weather fluctuations obscure genotype effects. Although omics approaches have generated abundant candidate genes, pathways, and markers, translation into breeding outcomes remains incomplete because protein-level validation is still limited, many associations remain correlative, and causal effects of sequence variation across tissues and environments are often unresolved. This gap is especially important in cultivated peanut because low genetic diversity, polyploid genome complexity, and limited transformation efficiency continue to hinder broad deployment of molecular breeding tools. Future studies therefore need integrated evaluation frameworks that jointly measure morphology, physiology, yield components, quality traits, and multi-omics responses under contrasting cultivation conditions. Such frameworks should combine high-throughput phenotyping, UAV and sensor-based field monitoring, genomic and epigenomic resources, and advanced computational modeling to identify robust markers and regulatory hubs that remain predictive across environments. They should also incorporate transcriptomic, proteomic, metabolomic, and phenomic information in order to resolve temporal and spatial stress responses more precisely and strengthen the linkage between genotype, molecular network behavior, and field phenotype. In parallel, functional validation using gene editing, genetic mapping, and multi-cultivar data integration will be essential to move from descriptive response profiling to causal understanding and practical cultivar design. Therefore, evaluating peanut under different cultivation conditions through a combined molecular and agronomic framework is both scientifically necessary and practically relevant, because it can accelerate the development of climate-resilient, resource-efficient, and high-quality peanut cultivars suited to increasingly variable production environments.

2 Effects of Different Cultivation Conditions on Peanut Growth and Agronomic Traits

2.1 Effects of planting density regulation on peanut canopy structure and yield formation

Planting density regulates peanut canopy architecture by altering leaf area development, light interception, and radiation use within the stand. Earlier work showed that planting pattern strongly affected leaf area index, canopy light interception, and pod and kernel yield, with approximately square arrangements intercepting light more efficiently than hedge-row arrangements at the same population density. More recent evidence indicates that density effects are not simply linear, because excessive crowding can increase canopy closure while reducing internal light penetration, weakening photosynthetic performance in lower canopy layers and increasing lodging risk (Zhao et al., 2022). This explains why density management should be viewed as a balance between rapid canopy establishment and maintenance of an efficient light environment throughout the reproductive period.

Yield formation responds to this structural balance. In Virginia-type peanut, optimal yield, radiation use efficiency, and pod maturity were generally achieved at intermediate densities of about 111 110-133 332 plants·ha⁻¹, whereas very low density delayed pod maturation and very high density could reduce yield under favorable moisture conditions. A separate density optimization study found that a sowing density of 2.85×10^5 plants·ha⁻¹ combined with growth regulation produced the highest yield by improving plant architecture, lodging resistance, and photosynthetic traits. Together, these results suggest that density-driven yield improvement depends less on maximizing plant number per se than on creating a canopy structure that sustains light capture, leaf function, and reproductive development.

2.2 Effects of water management on peanut physiological processes and yield formation

Water management directly influences peanut physiological activity, especially during flowering and pod filling when drought sensitivity is greatest. Under water stress, peanut showed marked declines in stomatal conductance, photosynthetic efficiency, and yield-related traits, with pod yield per plot reduced by 42%-44% and hundred-seed weight by 24%-38% in genotype evaluations under contrasting irrigation regimes (Macioszek et al., 2026). Physiological measurements under mulched drip irrigation similarly showed that appropriate irrigation increased net photosynthetic rate, transpiration rate, and stomatal conductance, whereas water deficit impaired photosynthesis and reduced shoot growth and yield formation. These findings indicate that water supply affects yield not only through biomass accumulation, but also through its control over gas exchange and assimilate production during key reproductive stages.

The agronomic response to irrigation is also shaped by irrigation scheduling and water-nitrogen coupling. In Turkey, the IF2I125 regime produced the highest seed yield among tested irrigation combinations, indicating that both irrigation frequency and irrigation amount must be optimized rather than maximized independently. Under Xinjiang mulched drip irrigation, the W2N1Q2 combination improved growth, yield, quality, and water-nitrogen use efficiency most consistently, showing that moderate, coordinated water and nitrogen supply outperformed zero-N controls and excessive inputs. Additional field evidence further suggests that deficit stress can be partly alleviated through hydrogel and glycine betaine application, which improved chlorophyll content, growth, and seed yield under reduced irrigation (Bakry et al., 2026). Overall, efficient water management in peanut requires synchronizing irrigation amount, timing, and accompanying inputs with crop demand across developmental stages.

2.3 Effects of nutrient supply and fertilization strategies on peanut production performance

Nutrient supply affects peanut production through combined effects on vegetative growth, nodulation, nutrient uptake, and partitioning to pods. Full recommended nitrogen combined with rhizobium inoculation and polythene mulch significantly enhanced growth, yield attributes, nutrient uptake, and profitability in irrigated peanut (Mondal et al., 2020). However, nutrient responses are not always proportional to fertilizer rate, because peanuts rely partly on biological nitrogen fixation and can experience reduced efficiency under imbalanced supply. This helps explain why fertilization strategies that integrate mineral nutrients with biological or organic amendments often outperform fertilizer-only approaches.

Evidence across fertilization studies supports an optimization rather than maximization framework. Multi-site trials in the North China Plain showed that regional mean optimal fertilization increased dry matter by 6.6% and pod yield by 10.9% relative to farmer practice while also improving nitrogen use efficiency and reducing unnecessary N and P inputs. In acidic red soil, pod yield increased with nitrogen up to 112.5 kg·ha⁻¹ but declined at higher rates, while calcium application further increased yield by enhancing photosynthetic rate and nutrient accumulation. Integrated nutrient management with recommended fertilizer, farmyard manure, and plant growth-promoting rhizobacteria also improved pod yield, haulm yield, and system productivity by strengthening root development and nutrient uptake (Jat et al., 2023). Thus, peanut production performance is highest when fertilization is matched to soil constraints, biological fixation capacity, and whole-system resource efficiency. In sum, planting density, water management, and nutrient supply each shape peanut growth and agronomic performance through their effects on canopy function, physiological activity, and assimilate allocation, and the most consistent gains come from optimized combinations rather than extreme single-factor inputs (Figure 1).

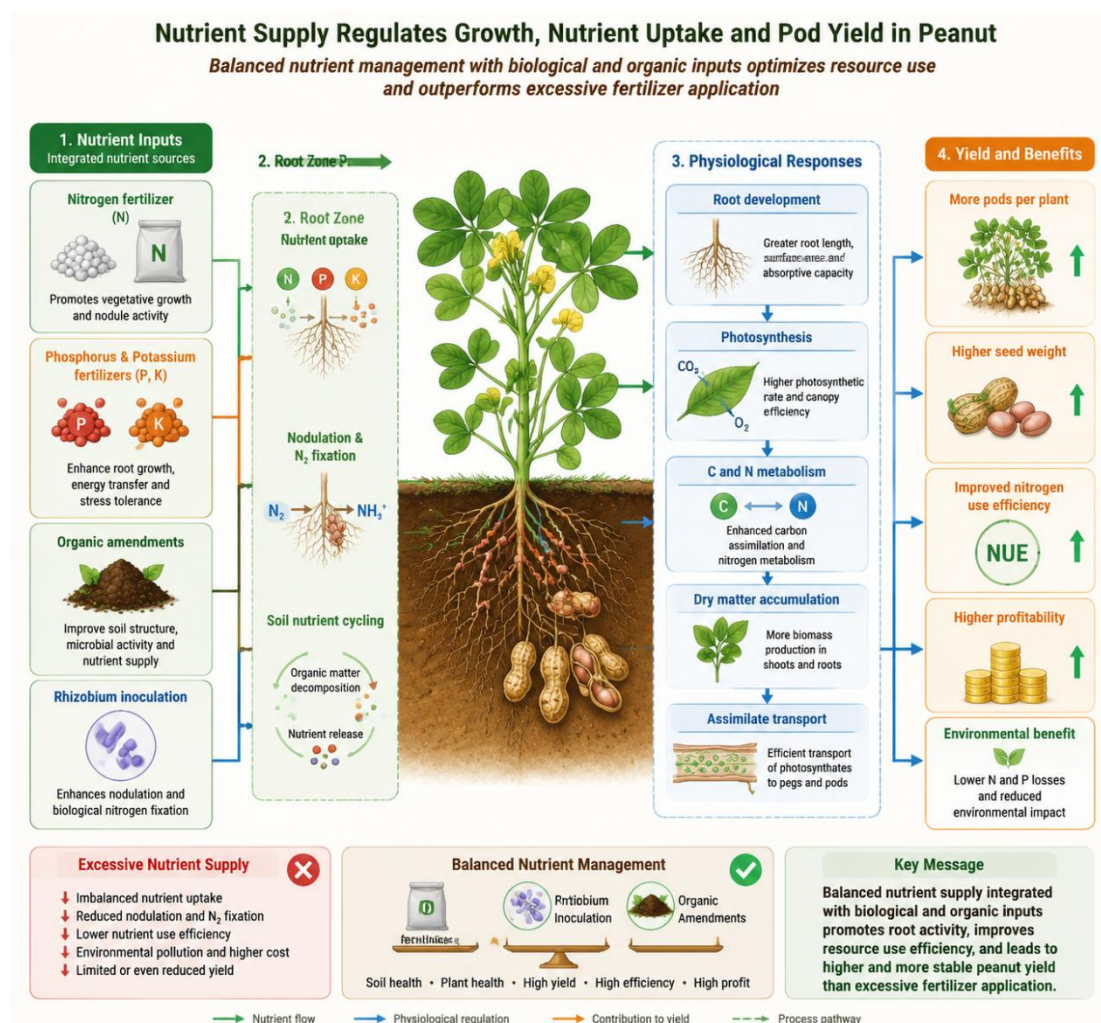


Figure 1 Mechanistic framework illustrating how nutrient supply regulates peanut growth, biological nitrogen fixation, nutrient uptake, and pod yield formation through coordinated physiological and resource allocation processes

3 Physiological Response Mechanisms of Peanut under Different Environmental Conditions

3.1 Photosynthetic regulation and carbon assimilation responses

Peanut photosynthetic regulation under changing environments is governed by both carbon supply through stomata and metabolic capacity within the chloroplast. Under progressive drought, stomatal conductance declines together with net photosynthesis, PSII quantum yield, and electron transport rate. However, drought limitation is not exclusively stomatal, because carboxylation capacity, electron transport capacity, and chloroplast CO₂ concentration also decline as stress intensifies, indicating substantial non-stomatal constraints on carbon

assimilation. Genotypic variation further modifies this response, as some water-saver types reduce photosynthesis early through stomatal closure, whereas biochemical limitations become more evident later in drought and differ among cultivars (Soba et al., 2024). This dynamic helps explain why stomatal conductance is a useful indicator of drought intensity but does not fully capture the carbon assimilation response of peanut.

Photosynthetic acclimation also depends on the broader environment, including atmospheric CO₂ and chilling conditions. Under elevated CO₂ in semiarid field conditions, peanut maintained high carbon assimilation alongside altered expression of carbon-metabolism genes, especially the downregulation of photorespiration-related transcripts (Laza et al., 2025). The same study showed that light reactions were strongly upregulated during water stress, while sucrose and starch metabolism was reprogrammed across developmental stages, indicating that carbon assimilation is sustained through coordinated adjustment of source metabolism rather than through a single pathway. Under nocturnal chilling, exogenous calcium improved photosynthesis by strengthening cyclic electron transport, balancing PSI redox status, and supporting ATP supply and photoprotection. Consistent with this, salt and osmotic stress reduce PSII efficiency and damage electron transport on the PSI acceptor side, showing that stress-induced limits to carbon assimilation in peanut often arise from disruption of photochemical as well as diffusive processes.

3.2 Root system architecture and rhizosphere interaction responses

Peanut root system architecture is a central determinant of environmental adaptation because roots integrate soil resource capture with whole-plant stress signaling. Root adaptation involves hormone signaling, antioxidant defense, osmolyte biosynthesis, and cell wall remodeling, which together regulate root depth, growth direction, and architecture under drought and salinity (Gelaye et al., 2025). Efficient root systems with deeper rooting and optimized xylem design improve water and nutrient acquisition under drought-prone conditions. Under acute drought, tolerant genotypes maintain higher root vigor and more lateral roots, while preserving root anatomical structure better than sensitive cultivars. These structural traits support continued resource uptake and help sustain aboveground physiological function when environmental conditions become restrictive.

Rhizosphere interactions further amplify the functional value of the peanut root system by reshaping microbial activity, nodulation, and nutrient cycling. Long-term crop diversification showed that peanut rhizosphere metabolite profiles changed through increased flavonoids and coumarins, which enhanced the growth and nitrogen-fixation activity of free-living bacteria and promoted *Bradyrhizobium* nodulation (Qiao et al., 2024). In maize-peanut intercropping, root interactions increased rhizosphere nitrogen-transforming enzyme activities and improved nitrogen fixation and transfer through microbial functional genes such as *nrfC* and *nirA* (Dong et al., 2024). Intercropping also increased isoflavonoid release from peanut roots and significantly enhanced rhizosphere *Rhizobium* abundance and *nifH* gene abundance, indicating that root exudation is an active regulator of peanut nitrogen acquisition. More recent evidence suggests that cereal-associated rhizobacteria can also optimize peanut root biomass and specific root length while improving nitrogen-use efficiency under continuous cropping stress.

3.3 Physiological defense mechanisms under abiotic stress in peanut

Peanut physiological defense under abiotic stress relies on coordinated osmotic adjustment, antioxidant protection, and hormonal signaling. Drought, salinity, and combined stresses stimulate the accumulation of sugars, starch, amino acids, and polyphenols, which contribute to osmotic homeostasis and cellular protection (Patel et al., 2022). Combined stresses that include heat intensify injury, producing higher electrolyte leakage and lower relative water content than single stresses, which shows that defense capacity is challenged more severely under multifactorial field-like conditions. At the signaling level, drought-induced ABA biosynthesis and downstream transcription factors coordinate stomatal closure, osmolyte accumulation, and antioxidant defense, linking metabolic protection with whole-plant water conservation. Similar integration is observed under salinity, where tolerant genotypes maintain Na⁺/K⁺ homeostasis and accumulate proline, sugars, and stress-related phytohormones to preserve cellular integrity.

Antioxidant defense is especially important because oxidative damage directly impairs membranes, chloroplasts, and root tissues under stress. Drought produces reactive oxygen species that damage chloroplast membranes and

reduce photosynthesis, whereas cultivars with stronger antioxidant production, including proline-associated protection, maintain healthier photosystems and better yield potential (Puppala et al., 2023). In peanut roots, tolerant materials show higher SOD and POD activities together with lower lipid peroxidation and H₂O₂ accumulation, which helps preserve anatomical structure under drought. Symbiosis with arbuscular mycorrhizal fungi strengthens this defense system by reducing ROS and MDA, improving leaf water status and photosystem protection, and promoting osmolyte accumulation and K⁺/Na⁺ balance under salt, drought, and cold stress. Transgenic evidence supports the same principle, as simultaneous expression of stress-responsive transcription factors improved membrane and chlorophyll stability through enhanced ROS scavenging and proline-mediated osmotic adjustment. Overall, peanut physiological responses under different environmental conditions depend on the integration of carbon assimilation control, root-rhizosphere plasticity, and stress-defense metabolism. Across these mechanisms, the most consistent pattern is that tolerance emerges from coordinated multi-trait adjustment rather than from any single physiological process.

4 Molecular Regulatory Mechanisms of Peanut under Different Cultivation Conditions

4.1 Regulation of environment-responsive gene expression

Peanut exposed to different cultivation environments shows extensive transcriptional reprogramming, especially under drought and salinity. Under severe drought, the number of differentially expressed genes increased progressively with stress duration, and enriched pathways included MAPK signaling, phenylpropanoid biosynthesis, glutathione metabolism, starch and sucrose metabolism, and plant hormone signal transduction. A separate drought transcriptome study likewise found that tolerant genotypes activated more genes associated with defense response, signaling, secondary metabolism, and circadian regulation than susceptible materials, indicating that stress adaptation depends on both the scale and specificity of transcriptional adjustment. These findings suggest that peanut gene expression under adverse cultivation conditions is not a simple on-off response, but a coordinated reorganization of regulatory and metabolic networks.

The environment-responsive transcriptome also differs by stress type, tissue, and regulatory layer. Under salt stress, peanut leaves displayed 3 425 differentially expressed genes, including 141 transcription factors from MYB, AP2/ERF, WRKY, bHLH, and HSF families, with enrichment in cell growth, cell wall organization, and antioxidant activity (Zhang et al., 2020). In roots, salinity induced an even broader multilayered response in which genes related to ion transport, osmolyte accumulation, and signal transduction were reprogrammed partly through DNA methylation changes, showing that epigenetic regulation contributes to environmental response in addition to transcription factor control (Pandey et al., 2025). Together, these studies indicate that peanut adapts to different cultivation constraints through stress-specific and organ-specific regulation of gene expression.

4.2 Hormone signaling-mediated growth regulation mechanisms

Hormone signaling is a core mechanism linking environmental perception with peanut growth regulation. Under simulated drought, transcriptomic evidence showed activation of both ABA- and SA-related pathways, while genes involved in reactive oxygen species clearance, osmotic adjustment, and protective structural changes were co-regulated with hormone signaling components. In another drought study, tolerant peanut genotype TAG-24 specifically activated plant hormone signaling genes such as PYL9, auxin response receptor genes, and ABA-associated regulators together with LEA proteins and glutathione reductase, indicating that hormonal control is integrated with dehydration protection and antioxidant defense (Gundaraniya et al., 2023). This coordination helps explain how peanut balances growth restraint with survival under fluctuating field conditions.

Specific gene families further clarify how hormone-mediated regulation operates at the molecular level. The NCED family, which controls a key step in ABA biosynthesis, contains drought-inducible members in peanut, and AhNCED1/2 were more strongly upregulated in the drought-tolerant cultivar NH5 than in the sensitive cultivar FH18 (Chen et al., 2024). Hormone-responsive transcriptional regulators are also broad in scope: AhTGA genes responded to drought, low temperature, and hormonal treatments, and overexpression of AhTGA11 enhanced cold and drought resistance by increasing antioxidant activity and changing endogenous ABA, SA, and JA levels. Additional family-level analyses showed that genes such as AhLOGs are induced by ABA, GA, IAA, MeJA,

drought, and salt, supporting the view that peanut growth regulation depends on extensive hormone crosstalk rather than a single signaling pathway.

4.3 Responses of metabolomics and proteomics under different cultivation conditions

Proteomic and metabolomic analyses show that molecular adaptation in peanut extends beyond transcript abundance to functional biochemical reprogramming. In a drought-resistant cultivar, iTRAQ proteomics identified 69 differentially expressed proteins, and the most enriched pathways were phenylpropanoid biosynthesis, flavonoid biosynthesis, and plant hormone signal transduction. Integration with earlier transcriptome data revealed overlapping gene-protein expression trends, including AhLEA2, and functional validation showed that AhLEA2 overexpression improved drought tolerance and altered antioxidant enzyme activity. These results indicate that drought-responsive proteins are not merely downstream markers, but active determinants of stress adaptation.

Metabolomic responses likewise point to systematic biochemical adjustment under different cultivation conditions. Recent integrative resources for peanut identified 2 035 metabolites across 22 tissues and linked multi-omics correlations to developmental and stress-related regulation, including prominent roles for IAA- and ARF-associated networks (Xue et al., 2025). Gene family studies further suggest that stress adaptation involves metabolic remodeling through enzymes associated with trehalose metabolism and secondary metabolism: AhTPS9 was strongly induced by cold stress and improved cold tolerance by regulating sugar-related metabolites and genes, while AhOMTs showed variable expression under hormone, water, and temperature stress, consistent with roles in secondary metabolic adjustment. More broadly, current multi-omics perspectives emphasize that combined transcriptomic, proteomic, and metabolomic analyses are essential for identifying root- and stress-specific molecular signatures that single-layer analyses often miss (Gelaye et al., 2026). Overall, peanut molecular responses under different cultivation conditions are shaped by stress-responsive transcriptional reprogramming, hormone-centered regulatory crosstalk, and multi-omics biochemical adjustment. Across drought, salinity, low temperature, and other field-relevant constraints, the most consistent pattern is that adaptation depends on integrated regulation across genes, proteins, and metabolites rather than on isolated molecular factors (Figure 2).

5 Comprehensive Evaluation Methods for Molecular and Agronomic Responses under Different Cultivation Systems

5.1 Evaluation system based on peanut phenotypic and agronomic traits

A comprehensive evaluation system for peanut under different cultivation systems should begin with multi-environment phenotyping, because yield, quality, and stress adaptation are all shaped by strong genotype-by-environment interaction. In a recent multi-environment study, nine yield and quality traits were evaluated across four environments, and all traits showed continuous variation, high heritability, and significant environment interaction, indicating that robust evaluation requires repeated field testing rather than single-site observation (Guo et al., 2024). Similar conclusions emerged from ecological-zone testing in China, where principal component analysis distinguished varietal performance patterns and lower coefficients of variation identified materials with more stable expression across environments. Therefore, field-based evaluation should integrate agronomic traits, quality traits, and stability parameters to capture both productivity and adaptability under contrasting cultivation conditions.

Trait system design should also include stress-specific indices and standardized measurement protocols. In salt-tolerance screening, researchers combined germination traits, seedling-stage salt tolerance coefficients, and field indices such as agronomic characters, yield traits, and SPAD values, then used principal component analysis, gray relational analysis, and weighted membership functions to derive comprehensive indices. Earlier QTL-oriented phenotyping in peanut similarly relied on standardized measurements of plant architecture, pod and seed dimensions, hundred-pod weight, hundred-seed weight, shelling percentage, and seed composition, and then used mean values across three environments to reduce environmental noise in trait characterization. Practical evaluation frameworks can also expand beyond yield alone: disease incidence scoring, harvest index, biomass, and postharvest quality traits such as aflatoxin accumulation have been jointly assessed in varietal trials, showing that production performance should be evaluated as a multidimensional trait set (Njoki et al., 2023).

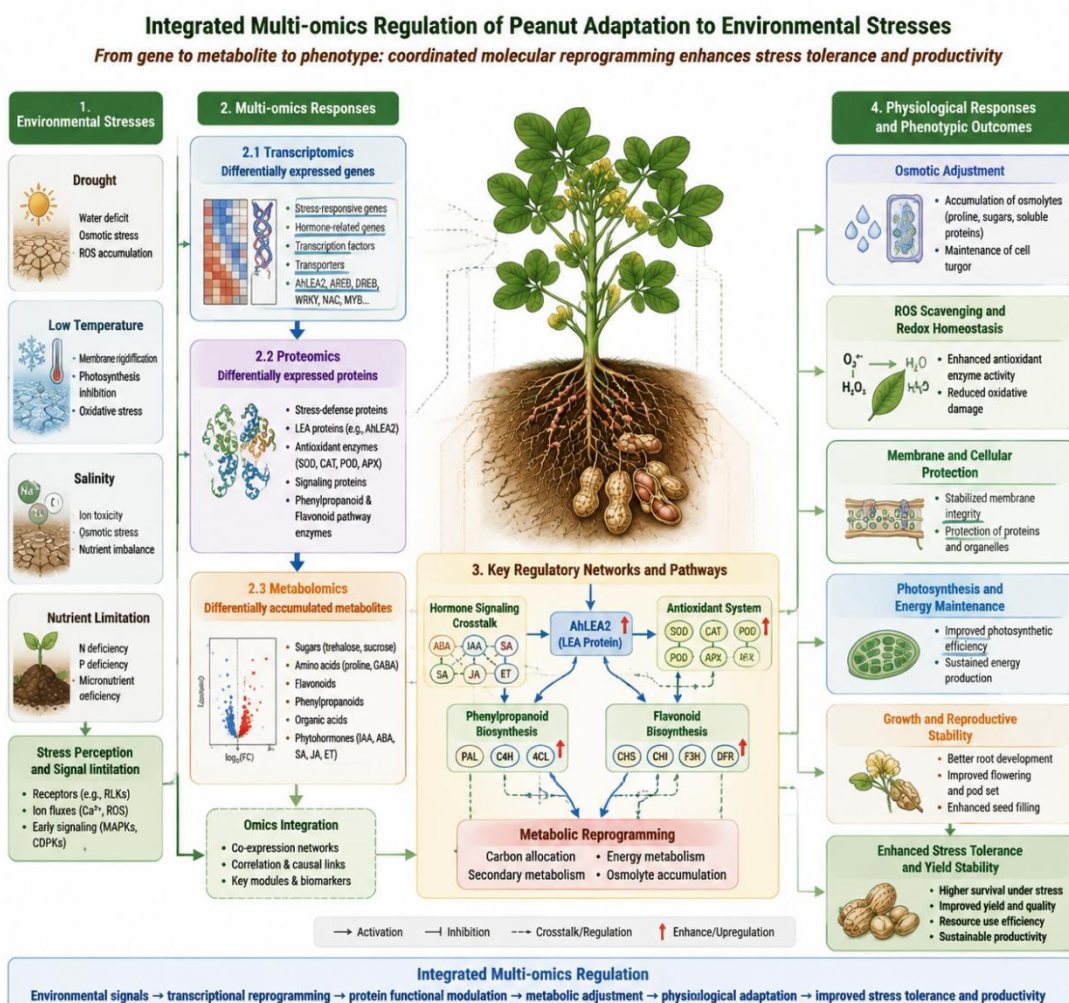


Figure 2 Integrated multi-omics framework illustrating transcriptional, proteomic, and metabolomic regulation of peanut adaptation under environmental stresses. The model highlights the coordinated roles of stress-responsive genes, functional proteins, metabolic pathways, and physiological adjustments in improving drought and stress tolerance

5.2 Molecular detection and multi-omics analytical technologies

Molecular evaluation of peanut responses under different cultivation conditions increasingly depends on integrated omics rather than single-layer assays. Current peanut omics frameworks include genomics, transcriptomics, proteomics, metabolomics, epigenomics, miRNAomics, and phenomics, and their joint use is considered essential for linking genome-scale variation to stress-responsive phenotypes (Huang et al., 2023). A major recent advance is the development of Peanut Omics, which integrates genomics, transcriptomics, proteomics, and metabolomics across 22 vegetative and reproductive tissues with biological replication, thereby enabling robust comparison of gene expression, protein abundance, and metabolite profiles throughout the life cycle. Such platforms strengthen candidate-gene discovery, biomarker screening, and functional network analysis in ways that isolated transcript or marker datasets cannot.

For cultivation-condition studies, the most informative analytical strategy is usually targeted multi-omics integration around specific stresses or management factors. Under NaCl stress, integrative transcriptomic and metabolomic analysis identified 1 470 metabolites and highlighted flavonoid biosynthesis, isoflavone biosynthesis, and plant hormone signaling as key pathways distinguishing tolerant and sensitive varieties. In peanut roots exposed to nitrogen deficiency and soil compaction, combined transcriptome-metabolome profiling detected 18 645 differentially expressed genes and 875 differentially accumulated metabolites, revealing coordinated shifts in amino acid metabolism, the TCA cycle, lipid metabolism, and isoflavonoid biosynthesis. Stress-combination metabolomics adds another layer of evaluation value, because principal component analysis, PLS-DA, and

heatmap analysis identified metabolites such as pinitol, malic acid, and xylopyranose as potential markers of combined abiotic stress responses.

5.3 Data integration and predictive modeling approaches

Because cultivation-system responses emerge from interactions among genotype, environment, and management, evaluation frameworks increasingly require integrated predictive modeling. Recent reviews show that combining multi-omics layers with environmental data is an important frontier for genotype-by-environment prediction, while tree-based methods such as random forest and XGBoost remain widely used because they are robust and relatively interpretable for small to medium agricultural datasets (Tsega and Mullualem, 2026). More broadly, predictive breeding frameworks now emphasize the joint use of omics, phenomics, and envirotyping to improve genotype-to-phenotype prediction for stress tolerance and crop performance. This means that evaluation is shifting from descriptive screening toward models that can forecast performance under specific cultivation regimes before extensive multi-year field deployment.

In peanut, remote sensing and machine learning already show practical value for high-throughput evaluation. UAV-based multitemporal phenotyping of canopy cover and canopy height enabled random forest and XGBoost models to estimate peanut yield, with random forest reaching an R^2 of 0.93 and proving useful for filtering underperforming genotypes in breeding pipelines. Hybrid frameworks that combine mechanistic crop variables with machine learning can further improve prediction, since adding crop-model features reduced yield-prediction error by 7%-20% in field agriculture and highlighted soil-moisture-related variables as especially informative. At the implementation level, scalable sensing, field-deployable sensors, and explainable ML are likely to be most useful when paired with interoperable data platforms and rigorous validation across environments, so that model outputs remain biologically meaningful and transferable to routine peanut breeding and cultivation assessment (Berlingeri et al., 2025). Overall, comprehensive evaluation of peanut molecular and agronomic responses under different cultivation systems is strongest when multi-environment phenotyping, integrated multi-omics detection, and predictive data modeling are used together. The clearest trend across the literature is a move from single-trait assessment toward systems-level evaluation that links field performance with molecular signatures and model-based prediction.

6 Case Study: Molecular and Agronomic Responses of Peanut under Different Water and Fertilizer Management Strategies

6.1 Case background and experimental design

Water and nitrogen regulation provides a useful case framework for evaluating peanut responses because both factors jointly determine growth, reproductive allocation, and resource-use efficiency under arid and semi-arid cultivation systems. Recent field studies in Xinjiang and Northwest China therefore adopted factorial water-nitrogen designs under mulched drip irrigation to capture the interaction between irrigation quota and fertilization rate in a production setting (Dong et al., 2025). A representative design included three irrigation levels, two nitrogen levels, and a no-nitrogen control, with treatment evaluation based on yield, water productivity, canopy or biomass traits, and quality indicators. Comparable regional experiments used irrigation quotas of 22.5, 30, and 37.5 mm with nitrogen rates from 77.5 to 110 kg/ha, showing that the case-study framework is well suited for identifying management thresholds rather than only single-factor effects.

At the mechanistic level, case studies of water-fertilizer interaction have also incorporated controlled-environment experiments to isolate short-term physiological and molecular responses. In one pot experiment at flowering stage, drought stress was set at $45\% \pm 5\%$ field water capacity and nitrogen treatment at 0 or 90 kg/ha, generating four groups that separated drought, nitrogen deficiency, and their combined limitation. Another controlled study examined the combined effects of water scarcity and nitrogen deficiency on peanut leaf physiology, photosynthesis, nitrogen allocation, and proteomic change, while noting that pot-to-field translation remains imperfect because water-nitrogen interactions are more complex under production conditions. This combination of field optimization and mechanistic pot experiments makes the case-study approach especially valuable for linking agronomic performance with underlying regulatory responses.

6.2 Effects of water and fertilizer regulation on peanut growth, yield, and quality

Across field studies, moderate-to-adequate irrigation combined with appropriate nitrogen supply consistently improved peanut growth, yield, and water-use performance. In Northwest China, optimized irrigation-nitrogen combinations increased pod yield by 25.13%-55.88%, oil content by 1.27%-3.56%, and water productivity by 26.74%-44.44% relative to the no-nitrogen control. In Xinjiang, the W2N1Q2 regime significantly improved main stem height, aboveground biomass, yield, protein, oil content, and water-nitrogen use efficiency, and obtained the highest composite score in principal component analysis. Similar evidence from an earlier mulched drip irrigation experiment showed that nitrogen application improved growth, physiological indices, yield, and water-use efficiency at the same irrigation level, while increasing irrigation under fertilized conditions further enhanced performance. Together, these findings indicate that peanut responds best to coordinated water-fertilizer regulation rather than maximal input of either factor alone.

The same pattern appears when quality and efficiency are evaluated alongside yield. In an arid-region deficit irrigation trial, severe deficit treatments reduced yield, economic return, water productivity, and kernel oil content, whereas DI20 increased water productivity by 17.1% with only marginal yield penalty, and the DI20N30 combination provided the best balance among yield, water productivity, net return, and quality (Rathore et al., 2021). Desert-oasis scheduling experiments likewise found that yield, water-use efficiency, and irrigation water-use efficiency were highest at 37.5 mm irrigation with 110 kg/ha nitrogen, while the contribution of water to pod yield and water-use efficiency exceeded that of nitrogen within the tested range. At a finer physiological scale, nitrogen application under drought increased biomass, relative water content, and pod yield by 12.10%, 36.84%, and 14.87%, respectively, showing that fertilizer can partly buffer drought injury when applied at an appropriate level. However, excessive nitrogen or mismatched water-nitrogen ratios can reduce efficiency and alter quality formation unfavorably, particularly by suppressing oil accumulation or lowering nitrogen partial factor productivity (Zhang et al., 2025).

6.3 Analysis of molecular responses induced by water and fertilizer conditions

Molecular analyses show that water and nitrogen treatments reshape peanut performance through broad transcriptional and metabolic reprogramming rather than through a single stress pathway. Under water and nitrogen co-limitation, peanut leaves displayed 5 294 differentially expressed genes, 324 differentially expressed transcription factors, and 829 known differentially accumulated metabolites. Drought-related genes were predominantly enriched in glycolysis/gluconeogenesis and glycerolipid metabolism, whereas nitrogen-deficiency-related genes were mainly enriched in starch and sucrose metabolism and amino acid biosynthesis. Under the combined constraint, secondary metabolite biosynthesis, transport, and catabolism accounted for a large proportion of responsive genes, indicating that dual stress induces a distinct regulatory state rather than a simple addition of single-stress effects. Broader drought transcriptomics in cultivated peanut supports this interpretation by showing enrichment in metabolic pathways, secondary metabolism, phenylpropanoid biosynthesis, and starch-sucrose metabolism in drought-responsive genotypes (Wang et al., 2021).

Proteomic and tissue-specific evidence further clarifies how these molecular changes connect to agronomic outcomes. Under water or nitrogen scarcity, leaf photosynthesis declined together with leaf nitrogen allocation to the carboxylation and electron transport systems, and several key photosynthetic proteins were downregulated, providing a mechanistic basis for reduced carbon assimilation and growth. Nitrogen supply can also act locally in reproductive tissues: pod-zone nitrogen application upregulated genes involved in nitrate transport and assimilation, including NR, NIR, GS, NADH-GOGAT, ABC, and NRT2, while increasing NR, GS, and GOGAT enzyme activities in pods. In roots, nitrogen deficiency altered amino acid metabolism, starch and sucrose metabolism, and the TCA cycle, whereas associated soil constraints such as compaction preferentially affected oxidoreductase activity, lipid metabolism, and isoflavonoid biosynthesis (Yang et al., 2022). Overall, the molecular case evidence indicates that successful water-fertilizer management in peanut depends on maintaining photosynthetic protein stability, nitrogen metabolic capacity, and flexible carbon and secondary metabolism across leaves, pods, and roots. In summary, this case study shows that optimized water-nitrogen coupling improves peanut agronomic performance while simultaneously reshaping transcriptomic, proteomic, and metabolic

responses across multiple organs. The clearest implication is that cultivation strategies should be evaluated not only by yield gain, but also by their capacity to sustain coordinated molecular regulation under variable water and fertilizer supply.

7 Applications and Prospects of Precision Cultivation and Molecular Regulation Technologies in Peanut Production

7.1 Precision cultivation management based on environmental sensing technologies

Environmental sensing technologies are becoming a practical foundation for precision peanut cultivation because they allow real-time monitoring of crop status, soil conditions, and field variability, thereby supporting more accurate irrigation, fertilization, and pest management decisions. In peanut systems specifically, remote sensing, GIS, GPS, and soil sampling have already been used to define management zones, and this site-specific approach reduced input costs and environmental impact through more efficient chemical use. More recent peanut-focused reviews also show that aerial and ground-based imaging platforms, together with AI-assisted analysis, are expanding from simple scouting into integrated crop health monitoring and targeted spray application (Asif et al., 2025). The main agronomic value of these systems is not just data collection, but the conversion of within-field heterogeneity into actionable management decisions at the appropriate spatial and temporal scale.

The next stage of precision management in peanut is shifting toward decision-support systems that combine sensing, phenology, and predictive analytics. For indeterminate peanut, non-invasive sensing and AI-based maturity assessment are especially important because conventional maturity evaluation is labor-intensive, spatially limited, and poorly suited to asynchronous pod development (Sahayaraj et al., 2026). Available evidence indicates that no single algorithm is universally optimal, but multivariate and machine-learning approaches become more robust when they integrate multi-source data rather than relying on a single vegetation index or platform. This pattern is consistent with recent peanut yield-prediction work showing that models including multiple phenological parameters outperform those based only on early-stage NDVI, with random forest achieving high predictive accuracy. Even so, broader adoption will depend on lower-cost sensors, user-friendly interfaces, stronger connectivity, and multi-environment validation before these tools can be deployed routinely across diverse peanut-growing regions.

7.2 Applications of gene editing and molecular breeding technologies

Gene editing and molecular breeding technologies are expanding the scope of peanut improvement by enabling more precise manipulation of complex traits than conventional selection alone (Umer et al., 2025). In recent reviews, CRISPR-Cas systems are described as especially important for modifying genes related to oil quality, allergenicity, and stress adaptation, while marker-assisted and genomic selection continue to accelerate improvement of yield, resistance, and quality traits in parallel. Experimental evidence in peanut already supports this direction: CRISPR/Cas9 combined with *Agrobacterium*-mediated pollen tube transformation successfully generated targeted mutations in AhMULE9A, and 11 of 15 transgenic plants carried protein-altering edits. These results are important because peanut's allotetraploid genome has traditionally made precise manipulation more difficult than in many diploid crops (Figure 3).

The future value of molecular breeding in peanut lies in combining editing tools with broader genomic and omics resources rather than treating them as isolated technologies. Recent syntheses emphasize that multi-omics platforms can identify resistance loci, stress regulators, and defense networks, while AI-assisted phenotyping can improve the efficiency of selecting edited or genomically predicted lines under field conditions (Pei et al., 2026). At the same time, important bottlenecks remain, including low transformation efficiency, genotype dependence, off-target concerns, and unresolved questions about field stability and long-term performance of edited traits across environments. Earlier work on peanut genetic engineering pointed to the same practical constraint, noting that regeneration efficiency and genotype dependence remain major barriers to routine transformation despite clear value for introducing stress- and disease-resistance traits. Therefore, the most realistic near-term prospect is not replacement of conventional breeding, but a hybrid pipeline in which editing, molecular markers, and field phenotyping are used together to shorten the path to resilient cultivars.

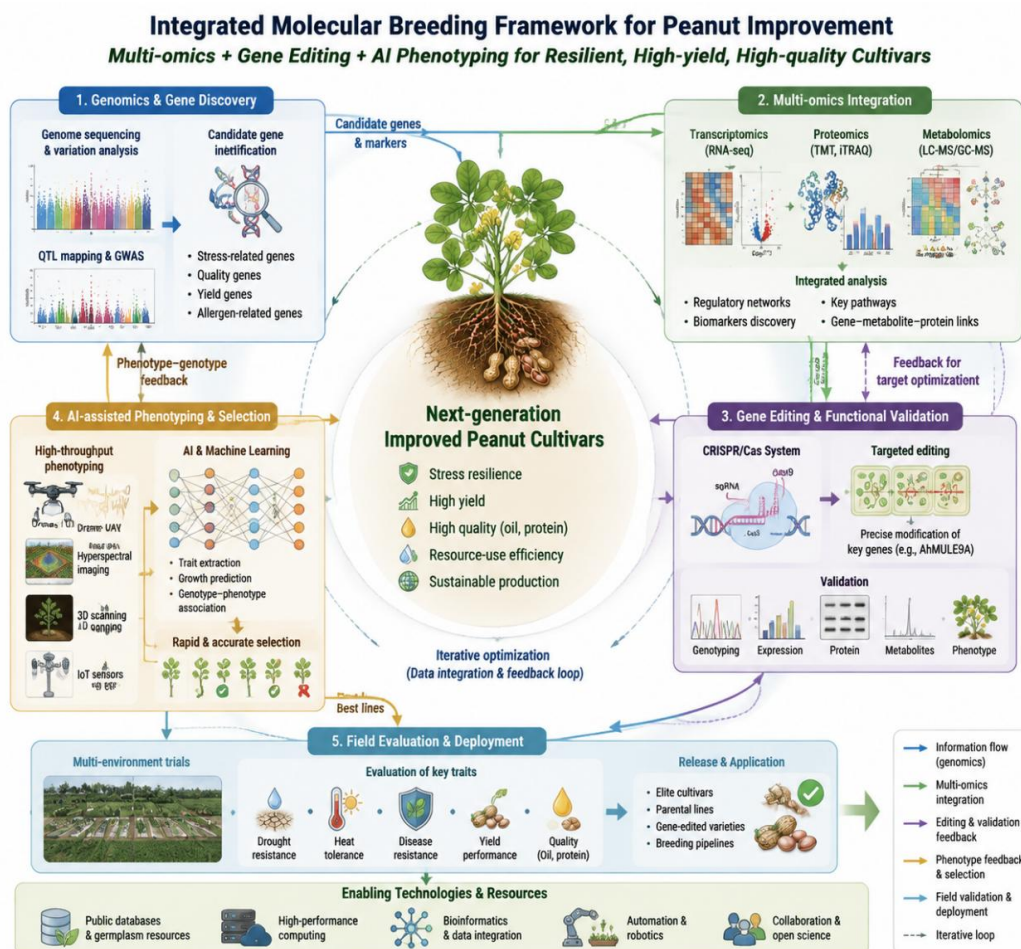


Figure 3 CRISPR-Cas-based molecular breeding workflow for peanut improvement, illustrating the integration of target gene identification, genome editing, regeneration, validation, and field evaluation for developing improved cultivars

7.3 Integration of molecular regulation and agronomic management strategies

The strongest future pathway for peanut production is the integration of molecular regulation with agronomic management, because field performance emerges from genotype, environment, and management interactions rather than from any single intervention. Current reviews increasingly argue for linking transcriptomic and metabolomic information with phenotypic and agronomic traits through computational modeling so that regulatory hubs can be connected to resource-use efficiency and stress adaptation in realistic cultivation systems. This integrated perspective is particularly relevant for root-mediated adaptation, where microbial interactions, root plasticity, and sustainable practices such as biofertilizer use and soil-health management are expected to complement genetic improvement (Gelaye et al., 2025). In this sense, molecular regulation is most useful when it informs how cultivation practices are adjusted, rather than being viewed only as an upstream breeding tool.

Several recent peanut-focused studies illustrate how this integration may work in practice. For example, pod maturity and preharvest sprouting risk are increasingly framed as traits that require joint management through hyperspectral imaging, soil and canopy moisture sensing, molecular markers, and adaptive decisions on sowing, irrigation, nutrient management, and harvest timing (Gelaye and Luo, 2026). Epigenetic evidence also suggests that peanut developmental responses to light, gravity, temperature, and soil conditions are mediated by DNA methylation, histone modification, and small RNAs, indicating that environmental management and molecular regulation intersect directly during peg elongation and pod initiation. Under multifactorial stress, future breeding and management frameworks will likely need high-throughput phenotyping, AI-assisted prediction, and multi-omics-guided identification of pleiotropic regulators so that agronomic interventions can be matched to cultivar-specific stress biology. Overall, precision peanut production appears to be moving toward a systems model in which sensing, molecular breeding, and adaptive field management operate as a unified decision

framework rather than as separate technological domains. In summary, the main prospect for peanut production is the convergence of environmental sensing, molecular breeding, and integrated agronomic regulation. The literature supports a shift from single-factor optimization toward data-driven, multi-scale management systems that connect field variability with molecular mechanisms and cultivar improvement.

8 Research Challenges and Future Development Directions

8.1 Insufficient understanding of peanut responses under multi-environmental conditions

stresses, whereas real cultivation systems expose plants to simultaneous and sequential combinations of drought, salinity, heat, nutrient imbalance, pathogens, and soil constraints. Root-focused syntheses further show that these combined stresses frequently produce nonlinear, synergistic, or antagonistic effects that cannot be predicted reliably from single-stress experiments alone. This limitation weakens both physiological interpretation and breeding relevance, because field performance depends on integrated whole-plant responses across roots, shoots, pods, and rhizosphere processes rather than on one stress pathway considered in isolation.

The problem is compounded by strong genotype-by-environment interaction and by the practical difficulty of phenotyping complex traits in field conditions. Drought tolerance in peanut is polygenic, and its evaluation is strongly affected by soil type, rainfall pattern, and weather variability, so cultivars classified as tolerant in one location may fail in another (Pokhrel et al., 2025). At the same time, omics experiments that truly mimic multi-stress natural environments remain difficult to perform, which is why most current studies still infer combined-stress biology indirectly from separate single-stress datasets (Calia et al., 2026). Future work therefore needs ecologically realistic experimental frameworks, stronger root and pod phenotyping, and broader use of wild *Arachis* germplasm to capture adaptive diversity that cultivated peanut lacks.

8.2 Challenges in multi-omics data integration and application

Multi-omics has clearly improved the study of complex crop traits, but its practical application in peanut remains limited by incomplete datasets, technical heterogeneity, and unresolved computational problems. Large-scale tissue-wide resources are still scarce in peanut compared with other crops, and the absence of comparable multi-scale platforms has constrained both developmental understanding and molecular breeding progress. More generally, integrative crop omics faces a persistent bottleneck in linking gene function, network behavior, and phenotype prediction across genomics, transcriptomics, proteomics, metabolomics, and environmental information. As a result, many studies remain descriptive and correlative rather than mechanistically causal.

Analytical limitations are equally important. Multi-omics datasets are high-dimensional and often affected by missing data, batch effects, and method-specific variability, which makes cross-platform integration and biological interpretation difficult (Hemme et al., 2026). In crop improvement studies, fewer than 20% of machine-learning integrations currently include environmental data for genotype-by-environment prediction, and fewer than 10% report calibrated uncertainty metrics, showing that prediction pipelines are still not mature enough for routine decision support (Tsega and Mullualem, 2026). Future development should therefore emphasize standardized data protocols, interpretable models, paired or staged integration strategies, and experimental validation using approaches such as CRISPR assays, spatial omics, and multi-cultivar comparisons to move from association to causation.

8.3 Development of intelligent peanut production systems for future agriculture

The development of intelligent peanut production systems will likely depend on combining sensing, connectivity, automation, and predictive analytics into a unified management framework. Precision agriculture already enables more efficient irrigation, fertilization, and pest management through real-time sensor data and IoT-supported decision-making. Broader Agriculture 5.0 perspectives extend this model by integrating AI, robotics, digital twins, big data, and advanced communication systems to support adaptive, data-driven crop management with lower environmental impact (Taha et al., 2025). For peanut, this direction is especially promising because below-ground pod development, variable maturity, and strong environmental sensitivity make conventional monitoring slow and labor-intensive.

However, intelligent production systems are not yet widely deployable, especially for resource-limited farming systems. Current reviews consistently identify high initial costs, data-management complexity, limited connectivity, and the need for user-friendly platforms as major barriers to adoption (Mansoor et al., 2025). Remote sensing and machine learning can improve yield prediction and resource-use efficiency at scale, but their broader impact still depends on scalable infrastructure, cloud computing access, policy support, and field validation across diverse agroecological settings. Looking ahead, the most effective peanut production systems will likely be those that integrate envirotyping, high-throughput phenotyping, multi-omics, and AI-assisted modeling into breeder- and farmer-facing tools that support both cultivar selection and real-time agronomic adjustment. Overall, the main future direction is a shift from single-factor analysis toward integrated, field-realistic, and data-driven frameworks for peanut research and production. Progress will depend on connecting multi-environment biology, causal multi-omics interpretation, and intelligent management systems into a single translational pipeline.

9 Conclusion

Different cultivation conditions exert a systematic influence on peanut growth, developmental coordination, and final yield formation. Planting density, water supply, nutrient availability, soil structure, and microclimatic variation collectively shape canopy architecture, photosynthetic efficiency, root development, reproductive allocation, and pod filling. These factors do not act independently; rather, they interact dynamically across developmental stages, determining whether vegetative growth is effectively converted into reproductive productivity. When cultivation conditions are properly matched to genotype and local ecological constraints, peanut plants can maintain better source-sink balance, improve dry matter accumulation and transport, and ultimately achieve higher yield stability. From an agronomic perspective, the effect of cultivation conditions on yield is expressed not only through pod number and seed weight, but also through the coordination of plant architecture, physiological activity, and resource-use efficiency. Excessive plant density may intensify intra-population competition and reduce light interception quality, while insufficient density can limit canopy productivity. Likewise, both drought and excessive irrigation can disrupt photosynthesis and assimilate partitioning, and improper fertilization may either restrict biomass formation or favor excessive vegetative growth at the expense of pod development. Therefore, high-yield peanut production depends on integrated regulation of cultivation factors so that growth conditions remain favorable throughout emergence, flowering, pegging, pod setting, and seed filling.

Peanut adaptation to different cultivation conditions is ultimately supported by coordinated molecular regulation. Environmental variation triggers changes in gene expression, hormone signaling, protein abundance, metabolite accumulation, and antioxidant defense, allowing plants to perceive external signals and adjust their internal physiological state. These molecular responses help maintain osmotic balance, protect membrane integrity, regulate carbon and nitrogen metabolism, and stabilize reproductive development under fluctuating conditions. In this sense, agronomic performance under stress or suboptimal management is closely connected to the efficiency and flexibility of molecular regulatory networks. The relationship between molecular responses and environmental adaptation is especially important because phenotypic resilience is rarely controlled by a single pathway. Instead, peanut tolerance to drought, salinity, nutrient limitation, and temperature stress arises from multilayered interactions among signaling systems, transcriptional regulation, metabolic remodeling, and tissue-specific developmental responses. Roots, leaves, pegs, and pods may each display distinct molecular adjustment patterns, yet these organ-level responses remain functionally integrated within the whole plant. As a result, environmental adaptation in peanut should be understood as a systems-level process in which molecular plasticity provides the mechanistic basis for physiological regulation, agronomic stability, and long-term productivity.

Future peanut research and production will increasingly rely on molecular technologies that can connect regulatory mechanisms with practical crop improvement. Advances in genomics, transcriptomics, proteomics, metabolomics, epigenetics, and phenomics are creating new opportunities to identify key genes, regulatory pathways, and biomarkers associated with yield formation, stress tolerance, quality improvement, and resource-use efficiency. At the same time, gene editing, molecular marker development, and genomic selection are

accelerating the transition from descriptive research to targeted breeding. These tools are expected to improve the precision of variety development and to support the design of peanut cultivars better suited to diverse cultivation environments. However, the long-term value of molecular technologies will depend on their integration with agronomic management and intelligent production systems. Sustainable and high-efficiency peanut production cannot be achieved by genetic improvement alone, because field performance emerges from the interaction of genotype, environment, and cultivation practice. Future development should therefore emphasize multi-omics data integration, high-throughput phenotyping, environmental sensing, predictive modeling, and field-scale validation under realistic management conditions. By combining molecular regulation technologies with precision cultivation strategies, peanut production systems can move toward greater productivity, resilience, input efficiency, and ecological sustainability.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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