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MOLECULAR MECHANISMS OF CHICKPEA RESPONSES TO DROUGHT STRESS (MINIREVIEW)

Purpose. *To analyze the current state and achievements in the research of chickpea genetics based on the trait "drought tolerance".* ***Results.*** *The importance of chickpeas for humans, animals and the environment is described. The information is provided on the distribution and harvest of chickpea in the world, including Ukraine, on the chickpea genome structure and the mechanisms of ensuring drought tolerance. The data on genetic basis of the "drought tolerance" in chickpea were analyzed. The necessity of a multi-omics strategy for the development of drought-tolerant chickpea varieties is shown. The examples of the successful use of molecular marker technologies for the creation of drought-tolerant varieties are given.* ***Conclusions.*** *The identification and using of regulatory gene-based markers provide a powerful strategy to accelerate marker-assisted breeding and ensure the development of chickpea varieties capable of withstanding increasingly variable climatic conditions.*

Keywords: *molecular markers, genetics, chickpea, drought tolerance.*

Introduction

Chickpea is not only excellent source of protein, significantly contributing to dietary protein intake and offering an efficient way to achieve the advised 1.5 cups of legumes weekly [1]. Chickpea protein is primarily utilized in various food products, including cereal-based items, bakery goods, infant foods, and meat products, with emerging potential in nutraceuticals. Its addition to cereal-based foods notably boosts the protein quality and overall nutritional profile, while also improving certain organoleptic aspects. Specifically, replacing a portion of wheat flour with chickpea flour in the products like pasta, bread, and other baked goods not only enhances their protein and nutritional content but may also improve their rheological, functional, and sensory attributes. Furthermore, chick-

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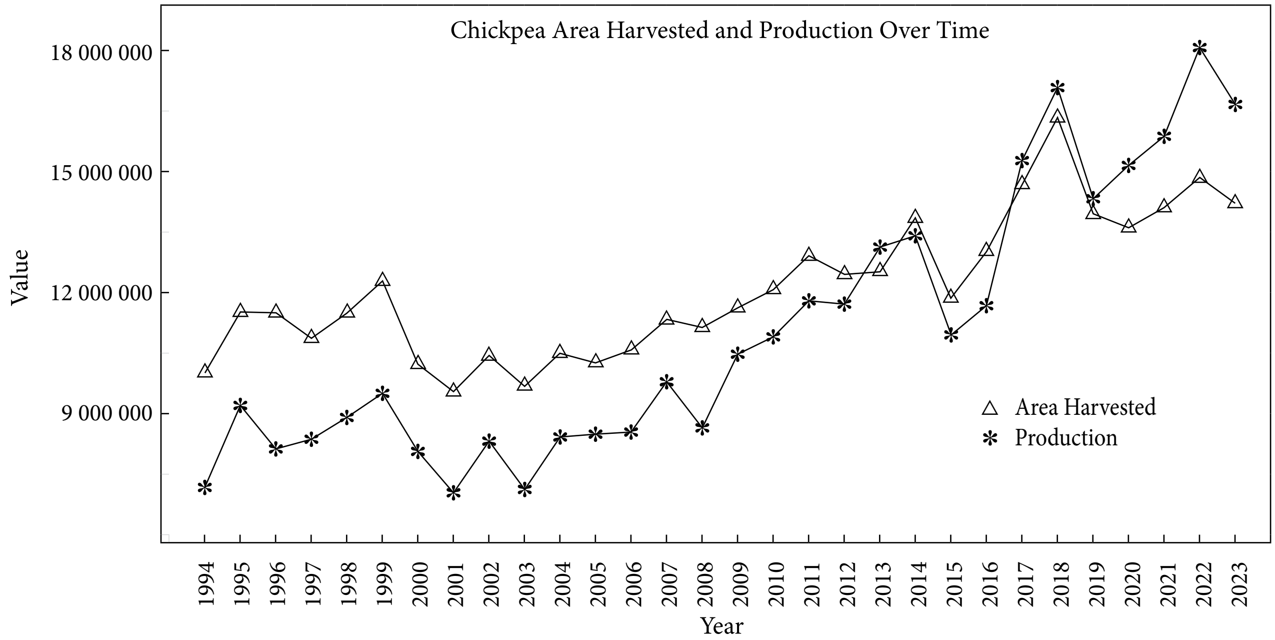

Fig. 1. Global area harvested (ha) and chickpea production (tons) over 1994—2023 period [3]

pea flour contributes to the development of low glycemic index pasta, catering to the dietary needs of diabetic individuals [2].

The global cultivation of chickpea saw an expansive harvested area, reaching approximately 14.81 million hectares and a substantial yield in terms of production, with a total output of roughly 18.10 million metric tons (Fig. 1). This production volume highlights the efficiency of chickpea farming practices and the crop's contribution to the global food supply, particularly in terms of providing a critical source of protein and nutrients. The data from 2023 reflects the ongoing efforts to enhance agricultural productivity and meet the dietary needs of a growing global population [3]. Average yield of chickpea shows increment grow and nearly doubled from 1994 to 2023 (Fig. 2), but nevertheless doesn't exceed 1,17 t/ha, meanwhile in Ukraine average yield of chickpea in 2023 was estimated as 1,55 t/ha [4] and by no means close to estimated genetic potential of chickpea under optimal conditions, which is 6,0 t/ha [5]. Drought represents a critical limitation to the chickpea production, accounting for up to a 50% decrement in yield and ranking as the second most substantial barrier. The yield outcomes are affected by a myriad of abiotic and biotic elements, among which drought stress stands out as a significant global detriment. Addressing this challenge, the development of shorter-duration cultivars and the improvement of water use efficiency emerge as vital strategies for mitigating the drought stress impacts on chickpea crops [6].

Agriculture stands as the sector most susceptible to climate change, given its extensive scale and acute sensitivity to meteorological variables, leading to substantial economic repercussions. Variations in climate-related phenomena, including temperature and precipitation patterns, profoundly influence crop yields [7], so investigation of molecular basis of the drought tolerance of chickpea is of the most importance to prevent the agriculture degradation due to climate change.

Chickpea genome structure. The genomes of the desi-type chickpea line 'ICC4958' [8, 9] and the kabuli-type line 'CDC Frontier' [10, 11] have

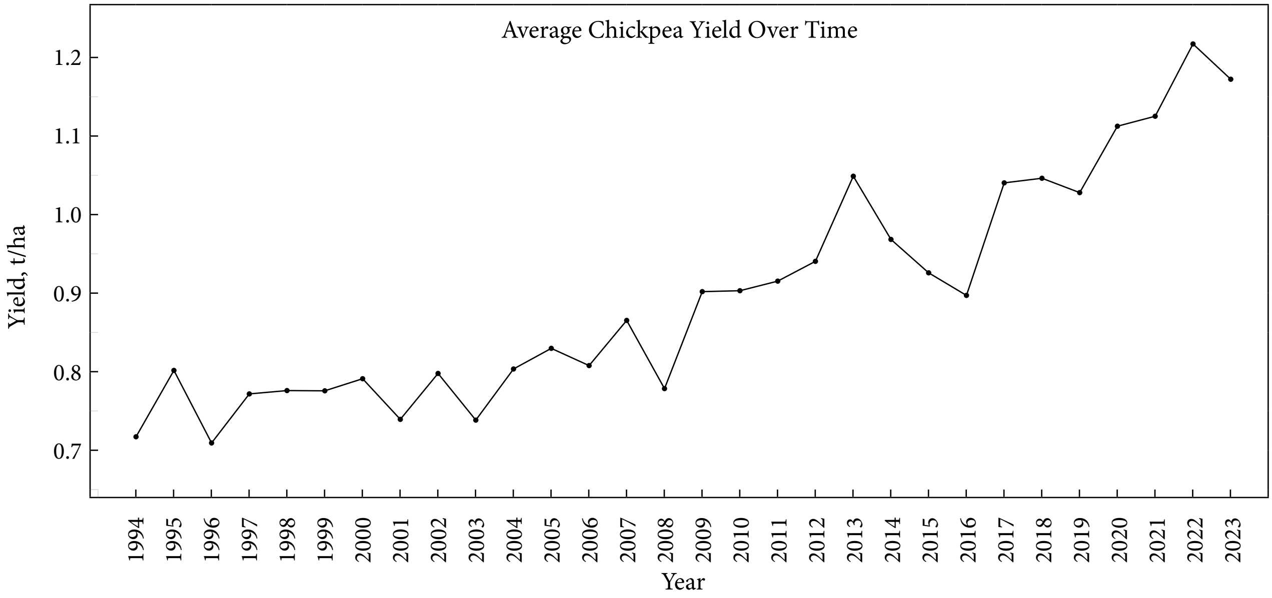

Fig. 2. Average yield of chickpea, dry in World, 1994—2023 [3]

been sequenced. The chickpea genome is estimated to be 738,09 Mb in size, 2n = 16, with 73,8% of the genome captured in scaffolds. Approximately half (49,41%) of the genome is composed of transposable elements and unclassified repeats, similar to other legumes like medicago, pigeonpea, and soybean. The centromere regions consist of microsatellites arranged as tandem repeats, with the most common unit repeats being 163-bp, 100-bp, and 74-bp repeats. A non-redundant set of 28,269 gene models was identified in the chickpea genome assembly, with an average transcript size of 3,055 bp and coding sequence size of 1,166 bp. In December 2024, version II of the sequencing results for the cultivar 'CDC Frontier' was published [12].

Pangenome study, based on the sequencing of 3,366 genomes provides a comprehensive genetic variation map. It encompasses detailed information on 3,171 cultivated and 195 wild accessions, offering a valuable resource for the chickpea research. The genome-wide association analysis pinpointed high-quality Single Nucleotide Polymorphisms (SNPs) in chickpeas, specifically targeting micronutrient concentrations like Zn, Cu, Fe, and Mn. It reveals significant genotype-environment interactions affecting nutrient concentrations across different genotypes [13].

A high-quality, full-length reference transcriptome assembly and expression atlas for protein-coding genes (PCGs) and long non-coding RNAs (lncRNAs), encompassing both vegetative and reproductive organs/tissues of chickpea, has been generated. The provision of a complete sequence set and expression profiles for PCGs and lncRNAs throughout development marks a substantial advancement towards the functional genomics of chickpea, including the assignment of functions to both coding and non-coding genome components. The findings underscore the expression dynamics and tissue specificity of PCGs and lncRNAs engaged in various biological processes integral to the characteristic key events of the respective tissues/organs. Additionally, transcriptome regulatory network (TRN) analysis sheds light on the gene regulation mechanisms operative across different tissues/organs. Analyses have elucidated the significant role of lncRNAs in the developmental biology of various tissues/organs and associated these lncRNAs with putative functions. Moreover, coexpressed lncRNA-mRNA pairs are identified, enhancing the functional characterization of the cis-regulatory potential of lncRNAs. The correlation of expression profiles/modules with quantitative trait loci (QTL) has identified the candidate genes potentially governing crucial agronomic traits, including seed size/weight and responses to abiotic stress, thereby offering a collection of prime target genes for further functional investigation. The datasets provided offer a comprehensive resource for extensive gene function studies and serve as a gateway for the genomics-enhanced improvement of chickpea [14].

The mechanisms of chickpea drought tolerance. There is a complex interplay of genetic factors, physiological responses, and molecular pathways that contribute to the drought tolerance in chickpea. Understanding these mechanisms is crucial for developing resilient crop varieties that can thrive under challenging environmental conditions. The drought effects in chickpea can be seen in different processes, such as photosynthesis, chlorophyll fluorescence, and water relations in both tolerant and susceptible genotypes. The problem of drought tolerance is multifaceted and complex [15]:

- *Drought stress effects*: Chickpea faces challenges from intermittent and terminal drought stress due to breaks in rainfall and limited moisture, impacting its growth and productivity significantly.
- *Genetic factors*: Various genes and proteins play a crucial role in conferring drought tolerance in chickpea, with specific physiological traits like early phenology and crop growth rate contributing to water conservation strategies.
- *Impact of drought*: Drought stress is a major cause of yield reduction in chickpea, accounting for around 50% of output losses globally. The severity, stage of crop, and duration of drought stress all influence the complexity of its impact.
- *Drought tolerance mechanisms*: Drought-tolerant chickpea varieties like ‘Gokce’ have been developed through gene pyramiding methods, showcasing traits such as early maturity, resistance to diseases, increased seed size, and suitability for harsh conditions.
- *Physiological responses*: Drought stress triggers various responses at physiological, biochemical, and molecular levels in plants. These responses can be categorized into six main categories: drought escape, avoidance, tolerance, resistance, abandonment, and adaptation.

Various studies have shown that the root traits, such as deep rooting, are closely linked to drought tolerance in chickpea. Genotypes with high root length density (RLD) have been found to produce higher yields under the drought conditions. Roots play a crucial role in regulating plant development under the drought stress. A well-developed root system can help plants cope with water scarcity by extracting moisture from deeper soil layers, thus enhancing their resilience to drought. The significance of root system development for enhancing the drought tolerance in chickpea, a crop susceptible to abiotic stresses like drought and salinity has been shown to be major factor, affecting both drought resistance and soil salinity resistance in chickpea [16].

The study investigated the relationship between various drought response traits and their association with the drought tolerance in chickpea. The order of traits identified as important and critical for drought tolerance were partitioning coefficient (closely related to harvest index (HI) and canopy temperature depression (CTD), crop growth rate (C), and phenology. Second-order traits, such as leaf area index (LAI) at mid-pod fill stage, pod number per unit area at maturity, and shoot biomass at reproductive growth stages, were relatively less important. The traits — reproductive duration (Dr), seeds per pod, and 100-seed weight were found to be least important. The study suggests that breeding for the best combination of partitioning and crop growth rate with the right phenology can result in the best CTD and grain yield under terminal drought [17].

Molecular genetics of drought tolerance in chickpea. The research on the drought tolerance in chickpea has identified several genes and transcription factors crucial for this trait. Numerous genes and transcription factors, linked with the drought tolerance in chickpea, have been identified. Some of the identified genes include *CarNAC4* associated with salt and drought tolerance, *CaNAC* linked to drought tolerance, *CarERF* involved in drought stress, and *CaSWEET* contributing to abiotic stress tolerance. The *ASR* gene was identified as a crucial transcription factor regulating drought stress tolerance. The studies demonstrated that the *ASR* gene activity, particularly NCBI Reference Sequence NP_001351739.1, enhances drought stress tolerance by regulating gene expression under drought conditions. The information about such genes and transcription factors is summarized in Table 1.

To elucidate the genetic underpinnings of the chickpea resilience to drought and heat stress, a thorough association mapping methodology was employed. This investigation resulted in the identification of 312 marker-trait associations (MTAs), with the greatest number of MTAs associated with the trait of 100-seed weight. The study revealed that linkage disequilibrium (LD), as measured by squared-allele frequency correlations (r^2), displayed rapid decay at a genetic distance of 5 centimorgans (cM) when r^2 was less than 0.20, and at a distance of 20 cM when r^2 dropped below 0.10. Within the context of 113 gene-based single nucleotide polymorphisms (SNPs), significant associations were discovered for six SNPs in the *ASR* gene, and three SNPs each in the *DHN* and *DREB* genes. These associations were linked with several phenotypic traits, including 100-seed weight, $\delta^{13}C$, plant height, root dry weight, pods per plant, and yield under the conditions of stress [18].

The observations indicated that the specific genes associated with various biological processes, including ethylene response, MYB-related protein activity, xyloglucan endotransglycosylase function, alkane hydroxylase MAH-like activity, BON-1 association, peroxidase 3 activity, the presence of cysteine-rich and transmembrane domains, vignain activity, and mitochondrial uncoupling, exhibited up-regulation in the drought tolerant genotype. Conversely, the same genes were found to be down-regulated in the genotype sensitive to drought. The interaction among different hormones and transcription factors that play roles in mediating drought tolerance and sensitivity in these genotypes highlights their potential as promising subjects for further investigation in the context of drought resistance research [20].

Forty aquaporin (AQP) genes were identified in chickpea and analyzed for various genetic and molecular characteristics [21]. This comprehensive analysis included assessments of genomic structure, protein sequence attributes, gene duplication events, phylogenetic relationships with *Arabidopsis thaliana* and other closely related legume species, three-dimensional models based on homology, and promoter sequences for the identification of conserved cis-acting regulatory elements. Additionally, the investigation of expression patterns of these *CaAQP* genes across different parts of the plant, as well as their responses to biotic and abiotic stressors, yielded significant insights into the roles of AQPs in mediating the osmotic stress responses in chickpea.

QTL-hotspot has been identified within chromosome 4 (Ca4), exhibiting significant influence on seed yield enhancements under rainfed conditions. The study delineates the contribution of the QTL hotspot to seed yield improvement through mechanisms such as augmentation of seed weight, acceleration of flowering time, modulation of traits pertinent to canopy development and early plant vigour, along with improved transpiration efficiency. The comprehensive analysis of whole-genome sequencing data, encompassing introgression lines (ILs) and their parental genotypes, pinpointed four genes residing within the QTL hotspot that are implicated in drought resilience. These findings underscore the potential utility of the identified candidate genes and superior haplotypes as focal points for genetic engineering and selection processes aimed at the advancement of chickpea cultivars [22].

Omics analysis of drought tolerance in chickpea. Employing an integrated multi-omics strategy enhances our understanding of the molecular

Table 1. **List of various genes/transcription factors and their roles in the response to drought and other abiotic stresses in chickpea [6]**

Gene / Transcription factor	Type	Function
DREB	Transcription factor (AP2/ERF family)	Binds to dehydration-responsive elements; regulates drought-inducible genes
Dehydrin (DHN)	Protective protein	Stabilizes cellular structures under water deficit; chaperone-like function
STPK	Protein Kinase / Signaling	Serine/Threonine protein kinase involved in drought stress signal transduction
CAD	Enzyme (Cinnamyl Alcohol Dehydrogenase)	Involved in cell wall lignification, which can impact stress tolerance (water loss, mechanical strength)
AMADH	Enzyme (Aldehyde Dehydrogenase)	Helps detoxify aldehydes formed under stress, linked with wound healing and abiotic stress response
TCS	Signaling (Two-Component System)	Mediates hormonal and stress signaling, including drought
EREBP	Transcription factor (AP2/ERF family)	Binds ethylene-responsive elements; modulates gene expression under stress
LEA Gene	Protective protein (Late embryogenesis abundant)	Maintains cellular stability during dehydration; high hydrophilicity
AKIN	SNF1-related Protein Kinase / Signaling	Positive regulator of drought tolerance through metabolic adjustments
Myb	Transcription factor	Regulates a broad array of stress-responsive genes
ASR	Small stress-responsive protein	"Abscisic acid stress-ripening" gene; modulates osmoprotection and ripening
SuSy	Enzyme (Sucrose synthase)	Catalyzes sucrose cleavage; important for osmolyte balance under stress
CAP2	Transcription Factor (DREB2A ortholog)	Binds drought/salinity-responsive elements; activates downstream stress genes
ERECTA	Receptor-like kinase	Regulates transpiration efficiency and plant architecture
SPS	Enzyme (Sucrose-Phosphate synthase)	Catalyzes sucrose biosynthesis; helps osmotic adjustment under drought
CAMTA	Calmodulin-binding transcription factor	Mediates Ca^{2+} signaling for salinity and drought tolerance
CarNAC4	Transcription factor (NAC family)	Regulates salt- and drought-responsive pathways
CaNAC	Transcription factor (NAC family)	Drought tolerance regulator; modulates stress-related gene expression
CarERF	Transcription factor (AP2/ERF family)	Regulated drought stress genes
CaSWEET	Transporter (Sugar transporter)	Facilitates sugar transport across membranes; confers abiotic stress tolerance via carbohydrate partitioning

mechanisms underpinning drought stress tolerance at a detailed level. The analysis of pathway enrichment, utilizing data from differentially expressed transcripts and proteins, indicated a significant role for pathways such as glycolysis/gluconeogenesis, galactose metabolism, and starch and sucrose metabolism in the drought-tolerant (DT) genotype. Comprehensive multi-omics investigations, encompassing transcriptomic, proteomic, and metabolomic data, identified co-expressed genes, proteins, and metabolites associated with phosphatidylinositol signaling, glutathione metabolism, and glycolysis/gluconeogenesis pathways, specifically in the DT genotype under the drought conditions. These pathways, responsive to stress, were synergistically modulated by the differentially expressed transcripts, proteins, and metabolites to mitigate drought stress effects in the DT genotype. Additionally, the genes, proteins, and transcription factors associated with QTL-hotspots could further augment drought tolerance in the DT genotype. Overall, the multi-omics approach yielded a comprehensive insight into the stress-responsive pathways and candidate genes for the drought tolerance in chickpea, presenting a valuable framework for future research and breeding strategies aimed at enhancing drought resilience [23].

Transcriptome analysis via RNA-seq was conducted on two genetically distinct genotypes, both under optimal conditions and following a week of drought stress exposure. The findings revealed that the genotype characterized by heightened drought susceptibility exhibited a more pronounced alteration in the gene expression compared to its less sensitive counterpart. Specifically, this genotype demonstrated upregulation of the genes associated with the photophosphorylation process, including transferases, oxygen lyases, and oxidoreductases, alongside genes linked to hormonal pathways (such as brassinosteroids, abscisic acid, and gibberellin responses), solute transporters, nutrient assimilation, and modifications in cell wall composition (evidenced by the upregulation of cellulose synthases, hemicellulose synthases, polygalacturonases, and pectate lyases). Conversely, the genotype exhibiting lower drought sensitivity showed a limited number of upregulated genes, predominantly those related to chromatin modifications, suggesting a different molecular strategy for coping with drought stress [24]. Analysis of this data revealed differences in alternative splicing (AS) between resistant and sensitive genotypes. AS represents a sophisticated regulatory mechanism that facilitates the generation of multiple mRNA variants from a single gene, leading to a broader proteome and increased functional diversity. This process is particularly significant in plants, where it plays a pivotal role in various biological functions, including development, signal transduction, and responses to environmental stresses such as drought. Through the induction of transcriptome plasticity, alternative splicing produces variant proteins that are crucial for maintaining cellular functions under the drought conditions. In chickpea, alternative splicing is a one of the regulatory mechanisms, enhancing the plant's resilience and adaptability to drought stress. A comprehensive understanding of these specific alternative splicing events and their functional outcomes is essential for the development of chickpea cultivars with superior drought tolerance. Such advancements are decisive for ensuring the sustainability of chickpea production and contributing to global food security in the face of increasing water scarcity [25].

Prospectives for marker-assisted breeding and conclusion. Taking into account the above, marker-assisted breeding (MAB) and marker-assisted selection (MAS) are promising approaches for developing varieties with desired traits, in particular, the chickpea varieties with increased drought tolerance.

One notable example is the introgression of the well-characterized "QTL-hotspot" region for improved root traits into elite chickpea backgrounds, thereby enhancing drought tolerance and ensuring stable yields. These efforts have led to the release of high-performing lines such as 'ICCV 93952', 'ICC 4958'-derived progenies, and other breeding materials that exhibit superior performance in drought-prone environments [26]. Genome-wide association studies (GWAS) have identified numerous SNP markers linked to drought tolerance and related agronomic traits. These markers are distributed across the chickpea genome and are associated with various traits such as seed weight, plant growth, and drought regulation. The identification of these markers facilitates the development of drought-tolerant chickpea cultivars through MAS [27—29]. MAB, in particular, has been strengthened by the availability of the chickpea genome sequence, allowing for more precise selection of the drought-tolerant traits. The integration of genomic selection models has also shown promise in increasing prediction accuracies for yield-related traits under the drought conditions [30].

The regulatory genes, which govern the expression of multiple downstream target genes, offer a particularly promising avenue for developing effective molecular markers in the chickpea breeding programs aimed at improving drought tolerance. By modulating critical stress-response pathways, these genes can exert a broad influence on plant physiology under water-limited conditions, controlling traits such as root architecture, stomatal conductance, and osmotic adjustment. Because the regulatory genes often coordinate the expression of diverse sets of defense and adaptation mechanisms, they can help breeders stack or pyramid multiple drought-responsive traits, leading to more stable tolerance across different environments. As a result, the identification and use of the regulatory gene-based markers provide a powerful strategy to accelerate MAS and ensure the development of chickpea varieties capable of withstanding increasingly variable climatic conditions.

In conclusion, marker-assisted selection and marker-assisted breeding hold great potential for improving drought tolerance in chickpea. Continued advancements in genomics and breeding technologies are essential to overcome the challenges posed by drought stress and to enhance chickpea productivity in arid environments.

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МОЛЕКУЛЯРНІ МЕХАНІЗМИ РЕАКЦІЇ НУТУ НА СТРЕС ВІД ПОСУХИ (МІНІОГЛЯД)

Мета. Проаналізувати сучасний стан досліджень і досягнень у генетиці нуту за ознакою «посухотолерантність». ***Результати.*** Описано значення нуту для людини, тварин і навколишнього середовища. Подано інформацію про поширення та збирання нуту у світі, в тому числі в Україні, про структуру геному нуту, механізми забезпечення посухотолерантності. Проаналізовано дані молекулярної генетики ознаки «посухотолерантність» нуту. Показано необхідність мультиомічної стратегії для створення посухотолерантних сортів нуту. Наведено приклади успішного використання молекулярно-маркерних технологій для створення посухотолерантних сортів. ***Висновки.*** Ідентифікація та використання маркерів на основі регуляторних генів забезпечує потужну стратегію для прискорення селекції за допомогою маркерів і забезпечення розробки сортів нуту, здатних витримувати дедалі мінливіші кліматичні умови.

***Ключові слова*:** молекулярні маркери, генетика, нут, посухотолерантність.