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Impact of Climate Change on Biomass Production

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Apstract: *An understanding of the bioeconomy's role in sustainable crop production is important. In order to focuses in optimizing biomass production under climate-induced stresses like drought and high temperatures an understanding of the physiological and molecular mechanisms crops are needed. How crops could adapt and survive under stress to ensure resource efficiency and economic resilience is provided in this review exploring the effects of drought stress and temperature fluctuations on agricultural crop growth, from cellular processes to whole plant responses.*

By examining adaptive mechanisms, such as changes in gene expression and metabolic adjustments, it offers insight into the strategies that crops use to survive and thrive under drought stress.

The provided review could help more understanding for the development of resilient cropping systems to ensure sustainable biomass productivity.

Keywords: Bioeconomy, Biomass Production, Climate Change, Drought, Heat, Crop, Physiological Response, Molecular Response

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4.1. The conceptualisation of the bioeconomy and biomass contribution

Bioeconomy is an economic model that applies to many sectors such as agriculture, forestry, fisheries, and industries that use biological resources to produce food, energy, materials, and products. It is centred around the sustainable production and use of biological resources as an important part of grand challenges in various fields such as climate change, food security, health, industrial restructuring, and energy security (Bugge et al. 2016; Stark et al. 2022). Unlike traditional economies, which rely heavily on fossil fuels, the bioeconomy aims to minimize environmental impact by integrating renewable resources, thus supporting sustainable economic growth and resilience. From a climate change perspective, a movement from fossil-based to bio-based products and energy is really important, but it also suggests that a transition to a bioeconomy will address the mentioned issues (Bugge et al. 2016; Stark et al. 2022; Toplicean and Datcu 2024). The Bioeconomy Strategy was launched in 2012 (EC 2013) emphasizing the important role of biomass production and the direct link between economy and environment (Fig. 4.1) for renewable energy sources.

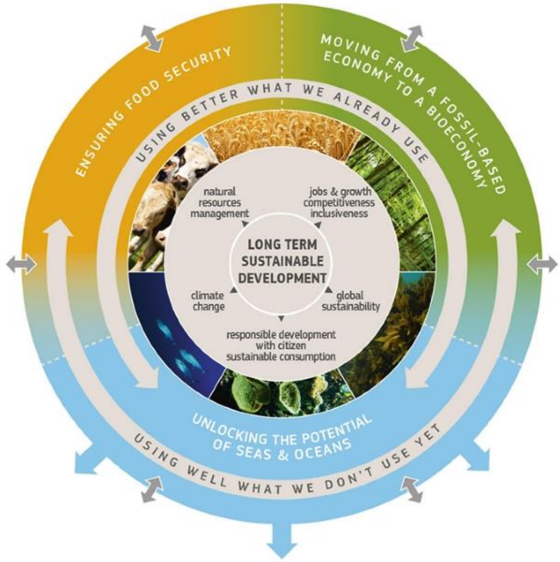

Fig. 4.1. Bioeconomy visual (https://knowledge4policy.ec.europa.eu/publication/updated-bioeconomy-strategy-2018_en)

Сл. 4.1. Биоекономија, визуелни приказ (https://knowledge4policy.ec.europa.eu/publication/updated-bioeconomy-strategy-2018_en)

In this sense, the role of the biomass production is important towards transition to climate neutral, circular bioeconomy (European Green Deal EC 2020) to provide food and materials for renewable energy. It is emphasized that the sustainability of production and consumption with better monitoring and control is the core of future biomass production and one of the most important bioeconomic strategies. A sustainable Bioeconomy for Europe: Strengthening the link between economy, society and the environment was updated on 2018 (EC 2018), providing the policy frame for implementing of a circular and sustainable bioeconomy in Europe. The conclusions from the updated strategy were adapted by the Council of the European Union in November 2019 and delivered a Bioeconomy Strategy Progress by 2022 (EC 2022). Report, from which, the EC developed the Progress Report "European Bioeconomy Policy: Stocktaking and Future Developments".

The conceptualizations of the bioeconomy in contents of climate change and contribution to addressing the main environmental challenges has been involved in studies before (Bugge et al. 2016; Stark et al. 2022; Toplicean and Datcu 2024). However, bioeconomy is still a very young and this field of study needs to be further developed and explained. In this content, the use of the bioeconomy in terms of the biomass accumulation under the challenging climate conditions need to be evaluated. The state of the European Bioeconomy and an assessment whether the implementation progress of the 2018 EU Bioeconomy Strategy and its Action Plan was identified, with the gaps and future opportunities of the bioeconomy policy, in light of recent policy developments within the European Green Deal.

Biomass contributes to sustainable crop production by creating value from crops by-products and reducing reliance on fossil-based products. The bioeconomy promotes crop production as an efficient use of biomass for multiple purposes, which play a central role for the bioeconomy development (Stark et al. 2022; Toplicean and Datcu 2024). Biomass consists of organic materials that can be converted into energy, chemicals, and other valuable products, often including crop residues, and even energy crops such as switchgrass or willow, grown specifically for bioenergy (biofuels or biodegradable materials), or plant-based fibers from hemp or flax that can be converted into textiles, insulating materials and packaging, reducing waste and creating circular systems within crop production practices. Crop residues can be returned to the soil to improve soil organic matter and fertility, promoting a closed-loop system (Wolf et al. 2023).

Crop biomass production refers to the accumulation of plant material and is a key component of the bioeconomy, where sustainable crop production plays a crucial role in energy, food security, and raw material supply (Stark et al. 2022; Toplicean and Datcu 2024). However, climate change poses a significant challenge to biomass production through its effects on temperature, precipitation patterns, and increased atmospheric CO_2 concentrations. To optimize biomass production under climate stress, farmers and agricultural systems need to adopt resilient strategies that enhance productivity while reducing vulnerability to drought and heat. Crop resilience to climate change is an urgent need and the ability of rapid advances in knowledge to provide solutions from crop management practices to gene editing to meet the future food demands of a growing global population (Benitez-Alfonso et al. 2023).

Although drought stress is one of the main factors for reducing biomass accumulation, it is often accompanied by high temperature, depends on the stages of crop growth and is most important in the reproductive growth stage (Calleja-Cabrera et al. 2020; Kuromori et al. 2022; Agho et al. 2024; Čereković et al. 2024). For this reason, it is necessary to develop more detailed perspectives of crop responses to drought stress for the possible increase in biomass accumulation in the next future due to global warming and water scarcity (Fig. 4.2).

Fig. 4.2. Artistic depiction of the problems and mitigation strategies surrounding the *impact* of heatwaves and drought on food security (Benitez-Alfonso et al. 2023), painting by Besiana Sinanaj, titled ‘Climate. Cultivation. Collaboration’

*Сл. 4.2. Умјетнички приказ проблема и стратегија за ублажавање утицаја топлотних таласа и суше на безбједност хране (*Benitez-Alfonso et al. 2023*), слика Бесиане Синанај, под називом „Клима. Култивација. Сарадња“*

A critical aspect of the bioeconomy is the use of biomass to effectively address global challenges with a more efficient allocation of biomass resources in challenging climate conditions (Thomchick et al. 2024). To improve biomass production, several approaches could be used to improve cropping and management such as crop rotation, mulching, efficient water management, development of drought and heat tolerant varieties and cultivars through selective breeding, and biotechnological approaches that overall support stable biomass production even in water scarce regions (Benitez-Alfonso et al. 2023). These crops are often engineered to have deeper root systems, faster growth rates, or greater water use efficiency, making them suitable for areas that face frequent droughts or extreme temperatures.

4.2. Crop physiological response to drought stress

Climate change affects the sustainability of crop production and biomass accumulation due to frequent periods of drought and increased temperatures (IPCC 2023; Čereković et al. 2010; Knezevic et al. 2018; Srdic et al. 2023; Čereković et al. 2024; Agho et al. 2024). During their life cycle, plants constantly face various adverse environmental conditions such as heat, cold, drought, and salinity, which cause significant physiological changes in plants and significant yield losses each year and it is going to increase in future due to climate effect (Shelake et al. 2022; Cui et al. 2022; Forster et al. 2024). Among all factors, drought stress is a key factor that affects biomass accumulation and can cause the most severe yield losses of immense economic importance (Hsiao 1973; Blum 2011; Seleiman et al. 2021; Čereković et al. 2024). Together with elevated temperature, it can significantly reduce transpiration and photosynthesis rates, which can significantly impact the vegetative and reproductive parts of the crop, thereby reducing biomass accumulation and yield (Seleiman et al. 2021; Kuromori et al. 2022; Rai et al. 2022; Čereković et al. 2024).

The physiological responses on the drought and temperature are numerous and may vary with the severity and stress duration. For example, during the maize crop growth, a decrease in biomass accumulation and grain yield was shown and particularly pronounced during the flowering and grain-filling stages (Lizaso et al. 2018; Čereković et al. 2019; Sheoran et al. 2022; Čereković et al. 2024). In future climate conditions, crop growth and development could be more affected by drought and heat stress (Lizaso et al. 2018; Li et al. 2022; Čereković et al. 2024; Aagho et al. 2024).

Crop responses during drought stress require system level analyses using genomic and physiological approaches (Chavez et al. 2003; Čereković et al. 2013; Čereković et al. 2014; Čereković et al. 2015; Fatnassi et al. 2018; Čereković et al. 2019; Seleiman et al. 2021). The severity of drought stress mostly depends on climate conditions, irrigation practices and soil moisture capacity (Hsiao 1973; Blum 2011; Seleiman et al. 2021). Plants under natural conditions (Chavez et al. 2003) can either be subjected to slowly developing water shortage (days to weeks or months) or face short term water deficit (hours to days). When plants are exposed to drought they can slowly or quickly develop a water deficit reaction (Chavez et al. 2003; Yang et al. 2021). Short-term physiological responses of plants under drought stress are stomata closure and root osmotic adjustment, while long-term responses are leaf osmotic adjustment, reduced transpiration area, and changes in shoot and root growth (Chavez et al. 2003). A summary of short-term and long-term responses of plants to drought stress is shown in Fig. 4.3.

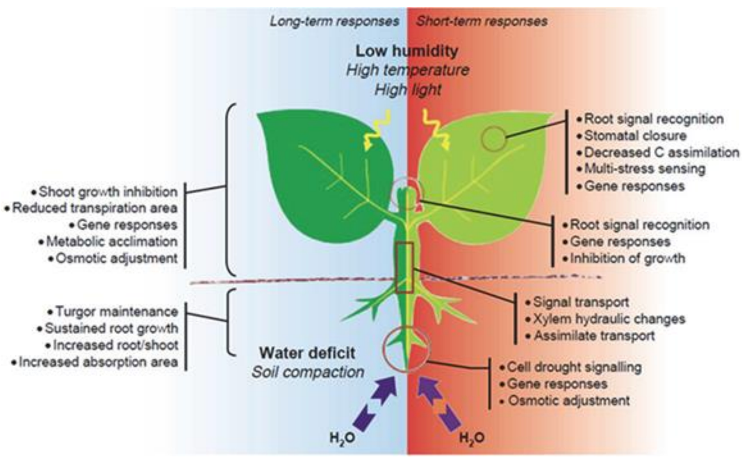

Fig. 4.3. Plant mechanisms of drought stress tolerance. Short-term responses (right) and long-term responses (left). (Chavez et al. 2003)

Сл. 4.3. Механизам отпорности биљака на стрес од суше. Краткорочни одговори (десно) и дугорочни одговори (лиево) (Chavez et al. 2003)

In general, the response of plants to drought stress can be roughly classified into three responses: a) short-term changes related to physiological responses mainly linked to stomatal regulation and leaf movement and positioning; b) acclimation to the availability of a certain level of water such as solute accumulation resulting from adjustments of osmotic potential and morphological changes; c) adaptation to drought stress conditions as modifications in anatomy (Schulze 1991; Kozlowski 1991; Pugnaire 1999).

As an escape strategy, when fast dehydration develops due to drought stress, plants try to escape and complete their life cycle before severe stress sets in. Thus, for this strategy flowering time is an important trait (Farooq et al. 2009; Shavrukov et al. 2017). Drought coping strategies typically involve a mixture of stress tolerance mechanisms such as stomata closure, osmotic adjustment, reduction of leaf area, and development of a large root system in order to maximize water uptake and minimize water loss to maintain higher water potential under water deficit conditions (Chavez et al. 2003; Seleiman et al. 2021). Drought stress is crucial in regulating stomatal movement where stomata closure is the most immediate response to drought stress and serves to reduce further water lost by reducing transpiration, but also results in lower CO_2 uptake affecting photosynthesis (Hsiao 1973; Čereković et al. 2013; Čereković et al. 2014; Čereković et al. 2015; Fatnassi et al. 2018; Čereković et al. 2019; Seleiman et al. 2021).

Crop response to temperature stress (Ali et al. 2020; Zhu et al. 2021; Agho et al. 2024) is associated with reductions in plant height, root length, biomass production and grain quality, as well as other effects (photosynthetic rate, stomatal conductance, transpiration rate, germination, anther dehiscence and pollination) which are similar to drought stress as shown in Fig. 4.4.

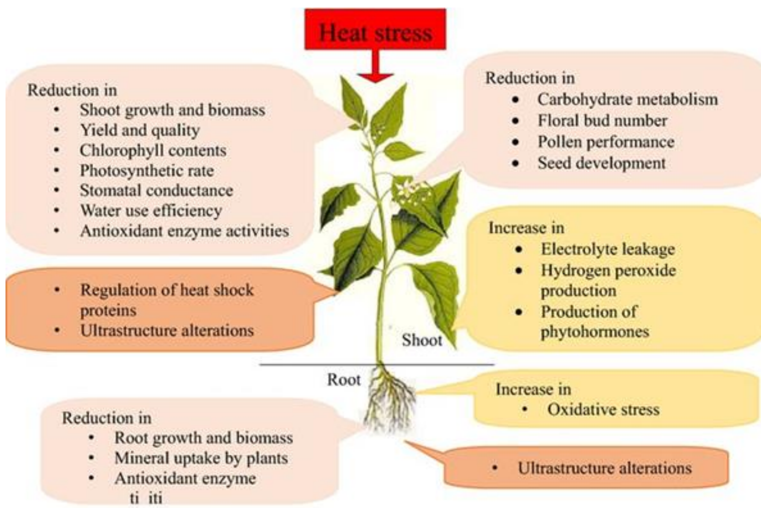

Fig. 4.4. Possible effects of heat stress on different parts of plants (Ali et al. 2020)
Сл. 4.4. Могући ефекти топлотног стреса на различите дијелове биљака (Ali et al. 2020)

The plant water status is indicated by leaf water potential, which is normally decreased due to drought stress and leads to growth inhibition (Čereković et al. 2013, Čereković et al. 2014; Gill et al. 2022). Crop physiological changes due to dehydration are presented in Fig. 4.5 and show at which water potential different physiological processes are affected.

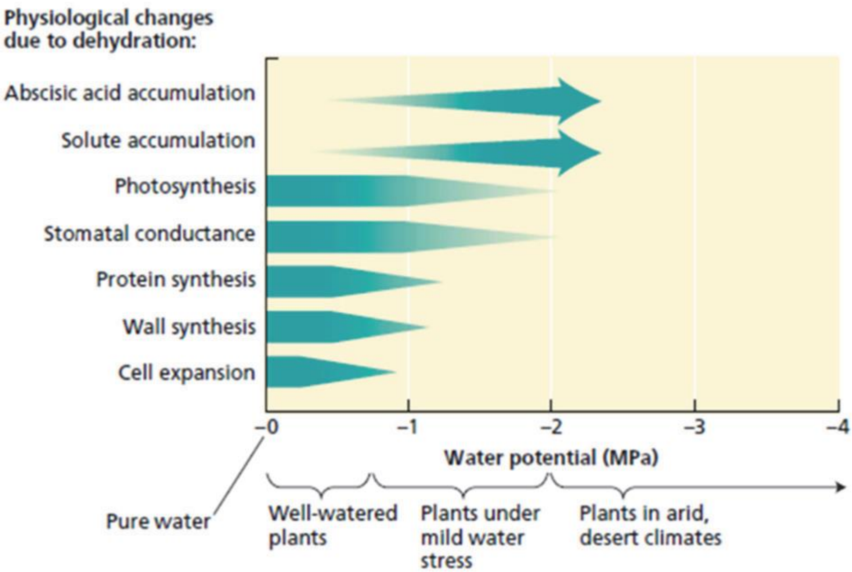

Fig. 4.5. Plant water potential under different growing conditions, and sensitivity of physiological processes to water potential (after Hsiao 1979)

Сл. 4.5. Водни потенцијал биљака у различитим условима гајења и осјетљивост физиолошких процеса на водни потенцијал (Према Hsiao 1979)

In osmotic adjustment solutes (proline, sugars) accumulate within the cells in response to a fall in the water potential (ψ_l) of the cell environment which results in the decrease in osmotic potential and help to maintain turgor and cell volume during drought stress (Chaves et al. 2003; Blum 2011; Čereković et al. 2013; Čereković et al. 2014; Čereković et al. 2019; Fatnassi et al. 2019; Seleiman et al. 2021). During stressful conditions, this could hold the water in cells, postpone dehydration, maintain growth and help the plant to sustain photosynthesis (Farooq et al. 2009; Seleiman et al. 2021). Osmotic adjustment is normally a slow process and fast onset of drought might not result in osmotic adjustment (Chaves et al. 2003; Blum 2017). In such situations, reduction in osmotic potential is mainly due to dehydration where osmotic adjustment only slightly contributes to turgor maintenance. Relative water content (RWC) is also an indicator of drought stress which represent the water content to full turgor, showing larger fluctuations for drought stressed plant compared to irrigated plants (Čereković et al. 2014; Soltys Kalina et al. 2016).

4.2.1. Climate change impact on vegetative plant growth

Rising temperatures and extreme weather conditions, especially drought stress, threaten crop production. Drought stress inhibits plant development and growth, which can result in morphological and developmental changes in affected organs, and reduced biomass, height and yield (Farooq et al. 2022; Gill et al. 2022; Čereković et al. 2019; Čereković et al. 2024; Agho et al. 2024). A decrease in photosynthetic activity and an increase in leaf senescence are associated with drought stress and adversely affect crop growth (Shao et al. 2008). Other effects of drought stress include a loss of turgor, reduced cell growth, cell enlargement and finally cessation (Shao et al. 2008). Leaf area reduction due to drought stress has been shown in many plant species (Farooq et al. 2009; Čereković et al. 2013; Čereković et al. 2014; Yang et al. 2021; Seleiman et al. 2021; Gill et al. 2022). Limitation in leaf expansion during drought affects growth as leaf area is usually proportional to photosynthesis (Chaves et al. 2003; Yang et al. 2021).

Stem growth inhibition has been studied less than leaf expansion, but growth inhibition occurs rapidly following the onset of drought stress (Yang et al. 2021; Gill et al. 2022). Roots play a critical role in overall plant health and yield stability, where deeper root systems are crucial traits for drought stress conditions (Ghatak et al. 2022). The root system as the interface between the plant and the growing medium is crucial for water uptake and its development, length and density are highly affected by drought stress (White and Kirkegaard 2010; Zhang et al. 2024).

Root-to-shoot biomass is a functional balance between water uptake by the root and photosynthesis by the shoot. It also reflects a balance between water uptake by the roots and the size of the water loss through shoot surface, maximizing the water absorbing biomass and reducing the water losing biomass (Zhang et al. 2024).

The total biomass of plants under drought stress is significantly reduced (Čereković et al. 2013, 2024) which leads to the production of smaller plants compared to irrigated ones (Fig. 4.6, 4.7). The shoot grows until it becomes too large that water uptake by the roots becomes limiting for further growth. At the same time, a root grows until their demand for photo assimilates from the shoot equals the supply (Taiz et al. 2010). In many droughts stress studies a decrease in the shoot to root ratio was observed (Blum 1996; Hsiao and Xu, 2000; Čereković et al. 2013; Seleiman et al. 2021) due to a relatively greater decrease in shoot weight compared to root mass (Blum 1996; Hsiao and Xu 2000).

Fig. 4.6. Plant development for non-irrigated (left) and irrigated (right) “Narve Viking” blackcurrant plants. (Photo: Krogh Damgaard C)

*Сл. 4.6. Развој ненаводњаване (лијево) и наводњаване (десно) биљке црне рибизле, култивар „Narve Viking“. (*Фотографија*: Krogh Damgaard C)*

Fig. 4.7. Plant development for fully irrigated (100%), deficit irrigated (50%) and rainfed maize crop, respectively. (Photo: Čereković N)

Сл. 4.7. Развој кукуруза приликом пуног наводњавања (100%), дјелимичног наводњавања (50%) и без наводњавања, респективно. (Фотографија: Чinvestigate Череković Н)

This indicates that shoot and root growth respond differently (Guasconi et al. 2023) where root growth being less sensitive compared to shoot growth at the same water potential may be due to greater osmotic adjustment in the extension region of roots compared to leaves (Hsiao and Xu 2000).

4.2.2. Climate change impact on reproductive plant growth

Climate change impact in future is a such a complex trait due to biophysical interactions and crop adaptations to abiotic stresses. The impact of climate change on sexual reproduction is the main cause of the reduction of biomass accumulation and the crop yield (Čereković et al. 2015; Lizaso et al. 2018; Sheoran et al. 2022; Čereković et al. 2024; Rivelli et al. 2024). Abiotic stress during reproductive stages can lead to significant reductions in both seed yield and quality, affecting their potential as renewable resources.

The understanding of plant responses to drought and temperature stress during reproductive development is very important as stress may significantly affect final yield (Figure 4.8).

Fig. 4.8. Drought and temperature stress impact on yield for non irrigated (left) and fully irrigated (right) maize crop, respectively. Photos: Čereković N

Сл. 4.8. Утицај суше и температурног стреса на принос ненаводњаваног (лиево) и наводњаваног (десно) кукуруза, респективно. Фотографије: Чepisode Черековић Н

Therefore, understanding the impact of climate change on the reproductive processes of crops is crucial for global food security and the prosperity of the bioeconomy (Benitez-Alfonso et al. 2023; Agho et al. 2024).

Drought stress accompanied with higher temperature profoundly affects flowering in crops where the reproductive phase is highly sensitive to water deficits, as water is essential for cell expansion and the development of flower tissues (Čereković et al. 2013; Čereković et al. 2015; Maple et al. 2024). Under drought conditions, plants may shorten the duration of flower development in an adaptive response to conserve resources. This often results in less interaction with pollinators due to the smaller flowers with lower quality and quantity of nectar, pollen grain sterility which results in decreased pollen viability, germination, and pollen tube growth (Kuppler at al. 2021). Moreover, water stress is particularly high at the grain-filling stages (Lizaso et al. 2018; Sheoran et al. 2022; Čereković et al. 2024) and can result in empty seeds or poorly filled grains, reduce grain set, smaller grain size and lower grain mass directly affecting both crop quality and yield. The sensitivity of flowers (Fig. 4.9) has been reported, and may result in flower abortion and consequently yield reductions (Čereković et al. 2013, 2015).

Fig. 4.9. Blackcurrant flowers for irrigated (left) and non-irrigatted (right) blackcurrant plants. Photos: Čereković N
Сл. 4.9. Цвјетови наводњаване (лијево) и ненаводњаване (десно) црне рибизле. Фотографије: Чepisode

Increased temperature during flowering reduces pollen viability and limits seed production, which are essential for crop improvement and sustainable biomass production (Rivelli et al. 2024; Maple et al. 2024). For example, for canola crops, growth stages such as flowering and seed development can have a greater impact on oil and protein concentrations compared to the vegetative development part (Secchi et al. 2023) which can limit productivity and growing demand.

4.3. Molecular mechanisms of crop response to climate change

Environmental stresses such as drought, salinity and high temperatures trigger a wide variety of plant reacions, ranging from altered gene expression and cellular metabolism to changes in growth rate and crop biomass production (Shinozaki and Yamaguchi-Shinozaki 2007; Huang et al. 2008; Čereković et al. 2015; Fatnassi et al. 2018; Čereković et al. 2019; Kuromori et al. 2022). The ability of bioenergy crops to withstand temperature extremes and drought stress is key to ensuring consistent biomass accumulation, especially as climate variability increases (Salgotra and Chauhan 2023). Lower reproductive success can hinder breeding programs aimed at developing drought and heat tolerant varieties with higher biomass yields.

The genetic and physiological responses of plants (Roy 2016) to these stresses involve a complex network of gene regulation, signalling pathways, and hormonal responses (Čereković et al. 2015; Roy et al. 2016; Fatnassi et al. 2018; Čereković et al. 2019; Salgotra and Chauhan 2023). Schematic representation (Fig. 4.10) illustrating exposure of plants toward different abiotic stress factors and the subsequent signal sensing, perception and transduction through sensors and associated signalling networks which result in the transcriptional activation of stress response genes through the involvement of various transcription factors including the MYB domain proteins. The epigenetic regulation of abiotic stress response via the activity of transcription factors has been indicated. (Roy et al. 2016)

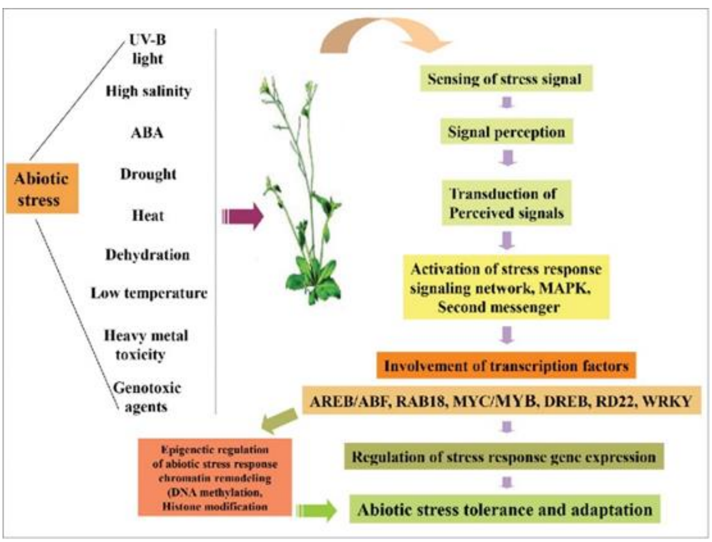

Fig. 4.10. Abiotic stress response and transcriptional regulation in plants

Сл. 4.10. Одговор на абиотски стрес и регулација транскрипције у биљкама

However, the understanding has rapidly progressed with the identification of thousands of genes that are induced during drought and temperature stress with a range of functions and roles in acclimatization and adaptation (Shinozaki and Yamaguchi-Shinozaki 2007; Huang et al. 2008; Čereković et al. 2015; Fatnassi et al. 2018; Čereković et al. 2019; Kuromori et al. 2022; Maple et al. 2024).

Gene ontology (GO) provides a structured vocabulary to describe gene functions across species, offering insights into the biological processes, cellular components, and molecular functions involved in stress responses. Cellular components refer to the parts of a cells or its external environment describing a location at the level of subcellular structure and macromolecular complex. Molecular function describes the biochemical activities of a gene product. Biological processes describe the participation by a gene product in operations or sets of molecular events with a defined beginning and end, pertinent to the functioning of cells, tissues, organs and organisms (Huang et al. 2008; Cohen et al. 2010). To understand the functional significance of over-represented functional terms of drought and temperature induced gene expression, Gene Ontology (GO) enrichment analysis can be used (Kakumanu et al. 2012, Čereković et al. 2015). Key GO terms frequently associated with these responses include stress response and genes related to response to abiotic stress, such as "response to water deprivation" and "response to temperature stimulus," which are common in drought and heat resistant plants. Regulation of transcription any stress-response genes are transcription factors, such as the DREB (Drought Responsive Element Binding) proteins, that regulate downstream genes are also involved in stress adaptation. Osmotic adjustment and cell wall reinforcement GO terms associated with osmolyte biosynthesis, cell wall remodeling, and lignin production are crucial, as these processes can help plants tolerate drought by maintaining cell structure and preventing water loss. In bioenergy crops, understanding these GO terms allows researchers to pinpoint specific genes or pathways to target for enhancing stress resilience.

Microarray studies, alongside next-generation sequencing technologies like RNA-seq, enable genome-wide profiling of gene expression under drought and temperature stresses (Slonim and Yanai 2009; Čereković et al. 2015). Gene expression studies offer insights into regulatory networks that control biomass accumulation under stress. These techniques reveal which genes are upregulated or downregulated in response to specific conditions (Ni et al. 2009). In bioenergy crops, microarray studies can identify unique expression profiles and novel stress-response genes that are not well-characterized in other crops, supporting targeted breeding for resilience. It could help in gene expression and metabolic changes in different tissues, stages of development and traits related to different environmental stresses (Ni et al. 2009).

The expression of Heat Shock Factors (HSFs) is related to various abiotic stresses including early heat stress, but since heat stress is often associated with drought it is likely that the up-regulation of HSFs was produced as indirect response to heat stress, as increase in leaf temperature influence stomata closure (Čereković et al. 2015; Andrási et al. 2021; Tian et al. 2021; Matkowski and Golec 2023). HSFs regulate the expression of Heat Shock Proteins (HSPs) which act as chaperones to ensure the correct folding of proteins. They bind and stabilize denatured proteins under stress conditions and prevent protein aggregation during heat stress (Matkowski and Golec 2023).

Many gene families and plant hormone pathways have important roles in responses to drought and temperature stress. Gene expression under drought and temperature stress is regulated by different hormones that have roles in several aspects of plant growth (Huang et al. 2008; Kuromori et al. 2022). Abscisic acid regulates a number of genes that are induced and have an integral role in drought stress signalling inducing the expression of stress related genes (Zhang et al. 2006; Shinozaki and Yamaguchi-Shinozaki 2007; Kuromori et al. 2022) and is the central hormone in drought response, mediating stomatal closure to prevent water loss and activating numerous drought-responsive genes (Aslam et al. 2022). Increased ABA (abscisic acid) production under drought helps bioenergy crops survive by limiting water loss but can also restrict growth, balancing survival and productivity. Most studies have shown that a key factor in controlling the downstream response to drought stress is ABA (abscisic acid) accumulation, and that both ABA-dependent and ABA-independent regulatory systems are involved in stress responsive gene expression (Li et al. 2020; Aslam et al. 2022). A CYP707A gene family encodes a hydrolase involved in ABA catabolism which has a major role in decreasing the ABA during drought conditions, thereby potentially controlling the plant ABA level (Seki et al. 2007; Degenkolbe et al. 2009; Li et al. 2020; Aslam et al. 2022). To help the plant to withstand abiotic stresses such as drought ABA interacts with other hormones (Aslam et al. 2022; Kuromori et al. 2024) including ethylene (ET), auxin (AU), cytokinin (CK), gibberellins (GA), salicylic acid (SA), and jasmonic acid (JA).

Ethylene production during drought stress is a signal to help plant to sense the stress and make in advance some adaptive physiological response. In that sense, when tolerant and sensitive crop varieties are compared, plants that produce low ethylene are more tolerant compared to those that produce higher levels (Čereković et al. 2019). Ethylene response factors (ERFs) trigger signal cascades by binding to ethylene response elements (EREs) in downstream genes and interact with the ABA insensitive4 (ABI4) to control plant response to drought stress (Fujimoto et al. 2000; Aslam et al. 2022). Ethylene increases in drought stress and is involved in controlling vegetative growth under different biotic and abiotic conditions (Chaves et al. 2003). Hence, a decrease in leaf growth and senescence due to drought and temperature stress could be due to increased ethylene signaling and overall reduced plant performance (Čereković et al. 2019; Fatma et al. 2022). It has been reported that root ABA accumulation during drought stress is high enough to antagonize ethylene and allow root growth, whereas in shoots, ABA accumulation is insufficient to antagonize ethylene, which inhibits growth (Sharp and Le Noble 2002). Auxin is important during flower organ development, axillary bud formation, root pattering and vascular tissue differentiation, leaf and root growth. As the expression of many auxin related genes are changed under dehydration, auxin may play an important role in plant responses to drought stress (Čereković et al. 2019; Kuromori et al. 2024). A decrease in auxin decreases the ABA level, which causes faster water loss further resulting in an increase of expression of some drought responsive genes (Chen et al. 2013). Cytokinins and gibberellins are plant growth regulators involved in different abiotic stresses, generally decrease under drought conditions, prioritizing stress survival over growth mediating plant tolerance to drought stress (Hai et al. 2020). Salicylic acid (SA), and jasmonic acid (JA) play roles in temperature stress tolerance, particularly in activating defense responses such as stomata closure (Kuromori et al., 2024). In bioenergy crops, optimized levels of SA and JA may help maintain biomass production under fluctuating temperatures (Zhang et al. 2024).

Cell wall-related genes and protein kinases also have regulatory roles in stress response and signal transduction (Qiang et al. 2000). Protein kinases function as receptors that after sensing of a signal such as drought stress transmit it into the cell (Shinozaki and Yamaguchi-Shinozaki 2007; Qiang et al. 2000). Transmembrane osmosensors like histidine kinases (AtHK1) may sense the changes in osmotic potential, whereas mitogen-activated protein kinases (MAPK) and Ca2+ – dependent protein kinase (CPK) cascades are used as a mechanism for relaying external signals to cellular control systems (Chaves et al. 2003; Zhang et al. 2006). Protein kinases and phosphatases are involved in osmosensor stimulation, and their genes are shown to be up regulated by drought stress. For example, 2C (PP2C) ABI1 and ABI2 protein phosphatases are known to be negative regulators of ABA signalling and in some specific mutations (e.g. abi1-1 or abi2-1) could cause ABA-insensitivity through alterations in their posttranscriptional regulation (Merlot et al. 2021). Cyclin-dependent protein kinases are activated by ABA-dependent and ABA-independent signalling pathways, involved in plant responses to drought stress and regulate stress responsive gene expression (Zhou et al. 2013).

Transcription factors such as MYB, and WRKY families are known to regulate drought and heat stress responses, often controlling suites of stress-related genes. Together with protein kinases and protein phosphatases, transcription factors are involved in further regulation of signal transduction and stress-responsive gene expression (Shinozaki and Yamaguchi-Shinozaki 2007; Chen et al. 2013). For example, drought inducible transcription factors MYC2 and MYB2 synthesis was promoted by ABA having an interaction between signalling pathways (Abe et al. 2003). Also, the transcription factors AREB 1 (abscisic acid-responsive element binding protein 1) and ABF (ABRE binding factor) bind to a cis-acting element ABRE (abscisic acid-responsive element) in downstream drought response genes such as RD29B, activating their transcription, and causing a range of physiological changes (Pardo 2010). They regulate signalling in drought stress tolerance and require ABA for full activation (Yoshida et al. 2010). Members of the bZIP family are known to bind to ABRE sequences and ABRE-like sequences and in turn activate ABA-dependent gene expression (Chen et al. 2013). The BZIP transcription factor has been shown in respond to drought and other abiotic stresses (Huang et al. 2008). The WRKY transcription factors are one of the largest families identified in various types of tissue (root, leaf, seed, inflorescence, abscission zone and vascular tissue) in drought, salt and pathogen infected conditions (Chen et al. 2013; Bakshi and Oelmüller 2014). The zinc finger transcription factor family have been identified in maize and respond to drought stress and ABA (Peng et al. 2012) and in Arabidopsis as an RNA-binding protein participating in flower development, abiotic and biotic stresses (Li et al. 2001).

Bioenergy crops are gaining recognition as essential components in climate change mitigation because they can serve as renewable energy sources, reducing reliance on fossil fuels and lowering greenhouse gas emissions (Stark et al. 2022; Toplicean and Datcu 2024). These crops have shown promise for generating high biomass yields. However, they remain largely undomesticated, meaning they haven't gone through extensive breeding and genetic optimization as food crops have, which limits the availability of well-adapted germplasm—collections of genetic material that breeders can use to improve crop resilience and yield (Benitez-Alfonso et al. 2023).

A primary benefit of bioenergy crops is that they can be cultivated on marginal land due to the lan competition, and where typical food crops may struggle due to poor soil quality, water scarcity, or other limiting factors (Khanna et al. 2021). This approach minimizes competition with food production, making bioenergy crops an attractive option in the broader sustainable crop production and energy landscape. However, new genotyping technologies must be applied to target drought-tolerant bioenergy crops and cultivars to help accelerate the development of renewable energy and the use of climate-resilient crops for the future.

To optimize bioenergy crops for biomass production, researchers are focusing on improving drought tolerance (Seleiman et al. 2021). Since drought stress can severely reduce biomass accumulation, and the gap between actual and potential yield is most often associated with drought stress, defining traits linked to drought tolerance becomes crucial (Čereković et al. 2013; Čereković et al. 2014; Seleiman et al. 2021; Farooq et al. 2022; Gill et al. 2022). These traits need to be measurable across large populations of genotypes—potentially hundreds or thousands—because the high genetic diversity within these populations allows breeders to select and propagate only the most resilient plants. Traits associated with biomass production under drought, such as root depth, water-use efficiency, and leaf area index, are often prioritized as they are directly linked to the plant's ability to maintain growth under water-limited conditions. Understanding the genetic basis of adaptation to drought (Allwright and Taylor 2015) is important and it has been identified for bioenergy crops (Taylor et al. 2019), such as *Populus* and *Miscanthus* (da Costa et al. 2019) and Arundo (Howarth et al. 2019).

For bioenergy crops, optimizing traits for biomass accumulation under stress involves targeting a combination of the gene networks and hormonal responses. New genotyping technologies, such as genome-wide association studies (GWAS) and genotyping-by-sequencing (GBS), play a vital role in identifying genes linked to drought tolerance (Allwright et al. 2016; Mathew et al. 2019; Habyarimana et al. 2020; Lee et al. 2023). These methods enable breeders to screen for genetic markers associated with desirable biomass production traits such as plant maturity (days to flowering), plant height, leaf area, stomatal index, dry mass fraction of fresh material and aboveground dry mass yield in bioenergy crops (Habyarimana et al. 2020; Allwright et al. 2016).

Integrating advanced genotyping and phenotyping methods can significantly accelerate the development of bioenergy crops that thrive in drought-prone regions. When combined with high-throughput phenotyping, which allows for the measurement of physical and physiological traits on a large scale, genomic selection becomes more precise and efficient. These technologies facilitate the identification of drought-tolerant genotypes that can then be used to breed crops optimized for bioenergy production under challenging environmental conditions to select genotypes that combine stress resilience with high biomass productivity (Hofman et al. 2024; Khuimphukhie et al. 2024).

The future of bioenergy crop breeding will likely include using climate-resilient cultivars specifically adapted to low-resource environments (Benitez-Alfonso et al. 2023). This approach not only supports renewable energy initiatives but also contributes to climate change adaptation by ensuring that bioenergy production remains viable despite increasing climate variability. Together, these approaches allow for a more holistic breeding strategy, aiming to produce bioenergy crops that not only withstand environmental challenges but also maximize biomass accumulation under suboptimal conditions, making them viable for renewable energy production and climate adaptation in the future (Dida 2024).

4.4. Conclusion

Biomass production plays a critical role in bioenergy and the bioeconomy, particularly under the challenges posed by climate change where drought and heat stress significantly impact both vegetative and reproductive crop growth. This is particularly pronounced during reproductive stages, which is of crucial importance given that understanding the physiological and molecular mechanisms is essential for improving crop resistance.

To improve biomass production under these conditions, sustainable strategies and biotechnological approaches are essential to contribute to solving global challenges by optimizing resource efficiency and supporting the economic resilience of agriculture within the bioeconomy.

Bioenergy crops offer a sustainable solution for renewable energy production, particularly through their ability to thrive on marginal lands where traditional food crops struggle due to poor soil quality, water scarcity, or other limiting factors. This approach reduces competition with food production and increases the role of bioenergy crops in meeting both energy needs and sustainability goals.

However, unlocking their full potential requires targeted efforts to develop drought-tolerant cultivars capable of maximizing biomass production under challenging environmental conditions. Further exploration and development of this field are vital to ensure sustainable crop production in the face of climate-induced stresses and soil conservation.

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Утицај климатских промјена на производњу биомасе

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Сажетак

Разумијевање улоге биоекономије у одрживој производњи култура је од изузетне важности. У циљу оптимизације производње биомасе под климатски изазваним стресовима, као што су суша и високе температуре, неопходно је разумијевање физиолошких и молекуларних механизама код пољопривредних и шумарских култура. Како културе могу да се прилагоде и преживе под стресом како би осигурале ефикасно коришћење ресурса и економску отпорност, објашњено је у овом прегледном раду, који описује утицај стреса изазваног сушама и температурним осцилацијама на раст култура, од ћелијских процеса до одговора цијеле биљке.

Испитивањем адаптивних механизама, као што су промјене у експресији гена и метаболичка прилагођавања, овај прегледни рад пружа увид у стратегије које културе користе за преживљавање у условима стреса изазваног сушом.

Значај рада се огледа у бољем разумијевању потребе за развојем отпорних система гајења како би се осигурала одржива продуктивност биомасе.

Кључне ријечи: биоекономија, производња биомасе, климатске промјене, суша, топлота, усјев, физиолошки одговор, молекуларни одговор