THESIS

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Effects of abiotic stress conditions on physiological performance of maize plant

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Abbreviations

PSI - photosystem I

PSII - photosystem II

CAM - crassulacean acid metabolism

WUE - water-use efficiency

ABA - abscisic acid

RWC - relative water content

ALA - 5-aminolevulinic acid

ROS - reactive oxygen species

PAR – Photosynthetically active radiations

AGB - above-ground biomass

BGB - below-ground biomass

RS - remote sensing

PSR - photochemical reflectance index

PSRI - plant senescence reflectance index

mNDVI - modified red edge normalized difference vegetation index

NIR – near infrared

P_n - net photosynthesis

P_m - maximum rate of photosynthesis

Rd - rate of dark respiration

TR - transpiration rate

LC - light curve

F_v - variable fluorescence

F_m - maximum fluorescence

1. Introduction

The need to raise crop productivity has grown considerably as a result of the world's population growth, the loss of arable land from soil erosion and urbanization, and the use of agricultural land for the production of biofuels (Godfray et al. 2010; Foley et al. 2011). Between 2005 to 2050, agricultural production is predicted to increase by 100–110% in order to meet the demands for calories per capita. The estimates correspond with the growth in real income per capita (Tilman et al. 2011). On the contrary, the yields of the three main crops wheat, rice, and maize which account for 57% of all agricultural production in terms of energy, are stagnant or declining (Ray et al. 2012). Threatening climate change is predicted to make this trend even more serious. These findings constitute a significant obstacle to our objectives of ensuring food security for every person on the planet while preventing more harm to the ecosystem. A crop's production efficiency is controlled by its critical processes and bringing about the desired physiological changes, which could improve plant photosynthesis and, consequently crop productivity (Wang et al. 2020).

Maize is one of the main world crops that is challenged by abiotic stresses like soil salinity, drought, and temperature fluctuations. Abiotic stresses that negatively impact plant growth processes include drought, excessive salt, heat, cold, UV radiation, heavy metals, and so forth. These stresses are thought to lower crop yields by over 50% (Rodziewicz et al. 2014). The three most harmful stressors that modern agriculture faces are drought, excess salt, and extreme temperatures. Drought is a major danger to food security, accounting for approximately 50% of crop failures and affecting 40% of arable land while salinity issues affect over 30% of irrigated land (Rehman et al. 2005; Kapoor et al. 2020). Plant reproduction, molecular function, and yield are all hampered by this complex abiotic stress (Kaur and Asthir 2017).

Photosynthesis and stress effects have been estimated using atmospheric satellite sensors from multiple missions (He et al. 2017). In order to gain a deeper understanding of the intricate relationships between stressors and crop characteristics, it is highly recommended to conduct observations across many spectral domains in addition to using a single remote sensing domain. Research on stress in precision agriculture has been connected to plant breeding initiatives and optical multi-sensor synergy (Berger et al. 2022). Vegetation indices (VI) were another promising technique for mapping changes in photosynthesis even from space. Calculating these indices, like the Photochemical Reflectance Index (PRI), require both proximal and remote sensing (F. Thenot and Winkel 2002). The VI relevant to P_n was similar to those critical to leaf chlorophyll content because of their indirect relationship to chlorophyll. Other vegetation indices linked to vegetation greenness and stress detection (mNDVI: Modified red edge Normalized Difference Vegetation Index) and carotenoid/chlorophyll ratio (PSRI: Plant senescence reflectance index) content are promising non-destructive methods for detecting yellow, stressed, and senescent plants (Merzlyak et al. 1999; Li and Guo 2018).

1.1. Objectives

The research is based on experimental studies and our primary aim is to evaluate the effects of different abiotic stress on physiological performance of maize. We will focus on alone drought and combined drought and heat stress under different treatments.

The study aims to:

1. To evaluate the light curve response of net photosynthesis in maize under different treatments.
2. Understand and examine what sorts of physiological changes occur in maize plants under nutrient deficiency and abiotic stress.
3. To assess parameters in both controlled and stressed conditions by using vegetation indices.

2. Literature review

2.1. Maize Production

Maize (*Zea mays* L.) is a significant staple cereal crop that is grown for food, feed and biofuel production all around the world (Miao et al. 2017). After wheat and rice, it is the third most important crop that is farmed. Studies have indicated that maize production needs to double, particularly in developing countries, to fulfill the growing need for food for humans and animals. The ideal temperature range for increased maize yield is between 28 and 32° Celsius, and 500 and 800 mm of water are needed to complete the life cycle (Xie et al. 2017).

In response to the growing global demand for primary crops, the volume of agricultural production worldwide has been steadily increasing over the past 20 years. The observed growth rate of 56% between 2000 and 2022 was made possible by advancements in production technologies and an intensification of farming practices, particularly the increased use of irrigation, fertilizers, pesticides, and high-yield crop varieties as well as the expansion of cropland despite the negative effects of climate change. The annual production change rate has experienced multiple ups and downs since 2000, with peaks ranging from 4 to 6 %. The only years it was negative were 2009 (-0.4 %) during the 2008 financial crisis and 2020 (-0.1 %) during the COVID-19 epidemic. The period's highest growth rate (+5.7 %) was recorded in 2011, following the 2009 downturn. Following 2013, the growth rates gradually decreased in magnitude, ranging from -0.1 percent in 2020 and 2.3 percent in 2017. In contrast to the pandemic's effects on global economic patterns, the 2020 downturn appears to have resulted from a decline in sugar beet and sugarcane production brought on by a confluence of unfavorable weather, governmental controls, and the yellow beet virus. In 2022, there was a 0.7% increase in crop output growth, which was caused by high inflation and general slack in the market following the start of the war in Ukraine (Fig. 1).

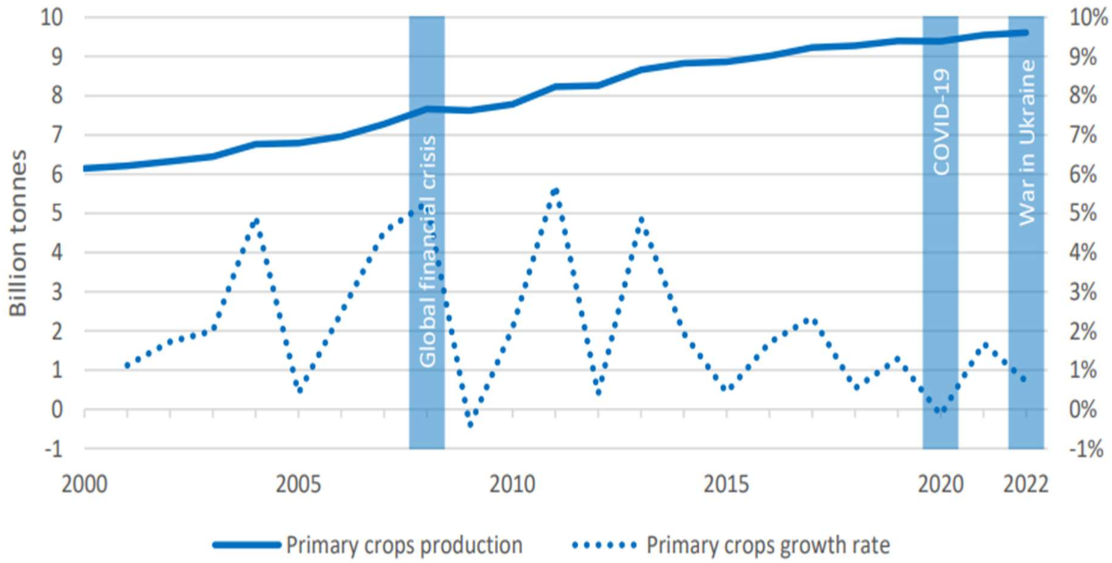

Figure 1: Global Agricultural Crops Production Source: (Brief 2022)

The top five cereal species produced in 2022 were maize, barley, wheat, rice, and sorghum. Compared to the other major grains, maize had the largest production (almost 1.2 billion tons) and the quickest growth since 2000 (+97 %). This is because maize is widely employed in sectors other than food, like animal feed and biofuels. However, between 2021 and 2022, maize production declined by 4% (to 44 million tonnes) due to a decrease in productivity in many European countries brought on by widespread drought as mentioned in (Fig. 2). The worst reduction in maize yield was recorded in Ukraine, where a severe 37 % decrease in yield was caused by a combination of weather and war.

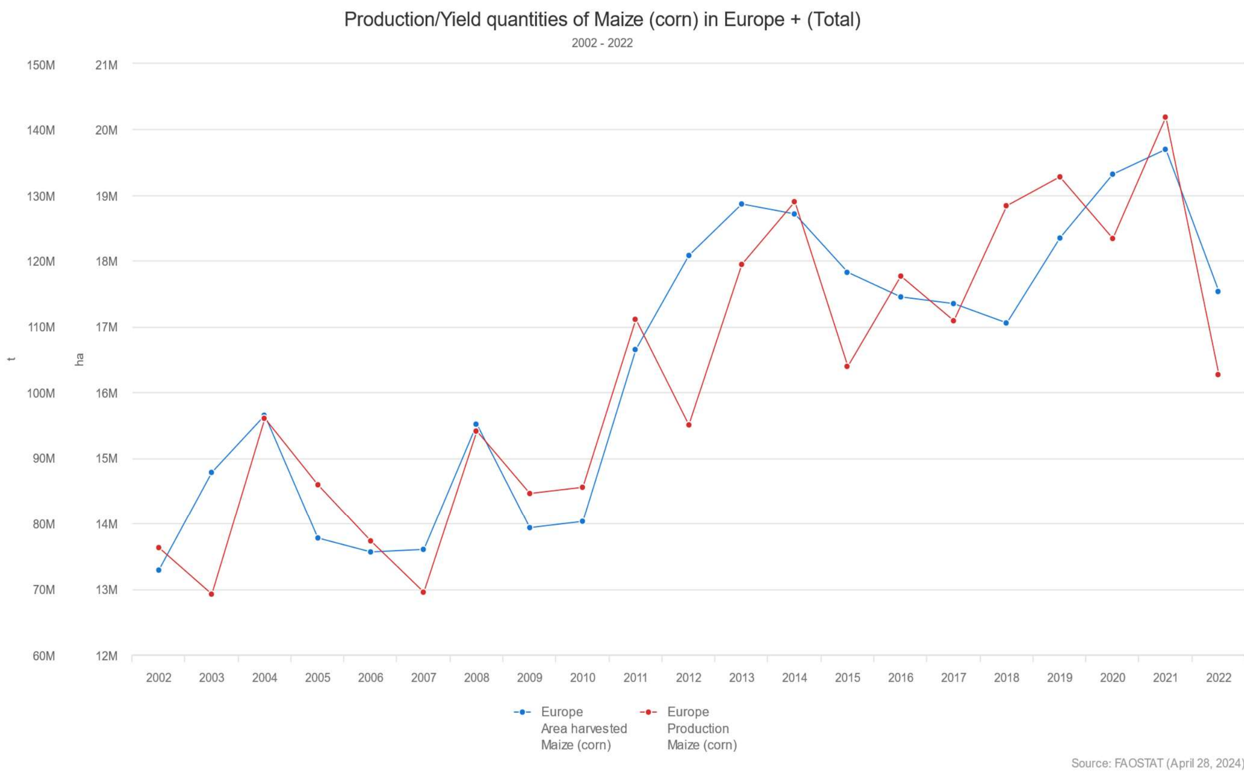

Figure 2: Maize production during the last two-decade Source: (FAOSTAT 2024)

The Americas contributed to 39 % of global yield of maize in 2022, with the United States and Brazil being the leading producing regions (Fig. 3). With a 24 % share, China was the second-largest producer.

Since the variability in maize yield is increasing due to changing climatic circumstances, understanding the overall effects of climate change on the growth and development of this staple crop is essential to forecasting its production. Among the various abiotic stressors, temperature extremes, droughts, nutrient deficiencies, and salinity are thought to be the primary environmental factors reducing maize yield overall. According to recent research, the two most significant climatic variables are temperature and precipitation, with radiation playing a crucial role in determining its yield (Xu et al. 2016).

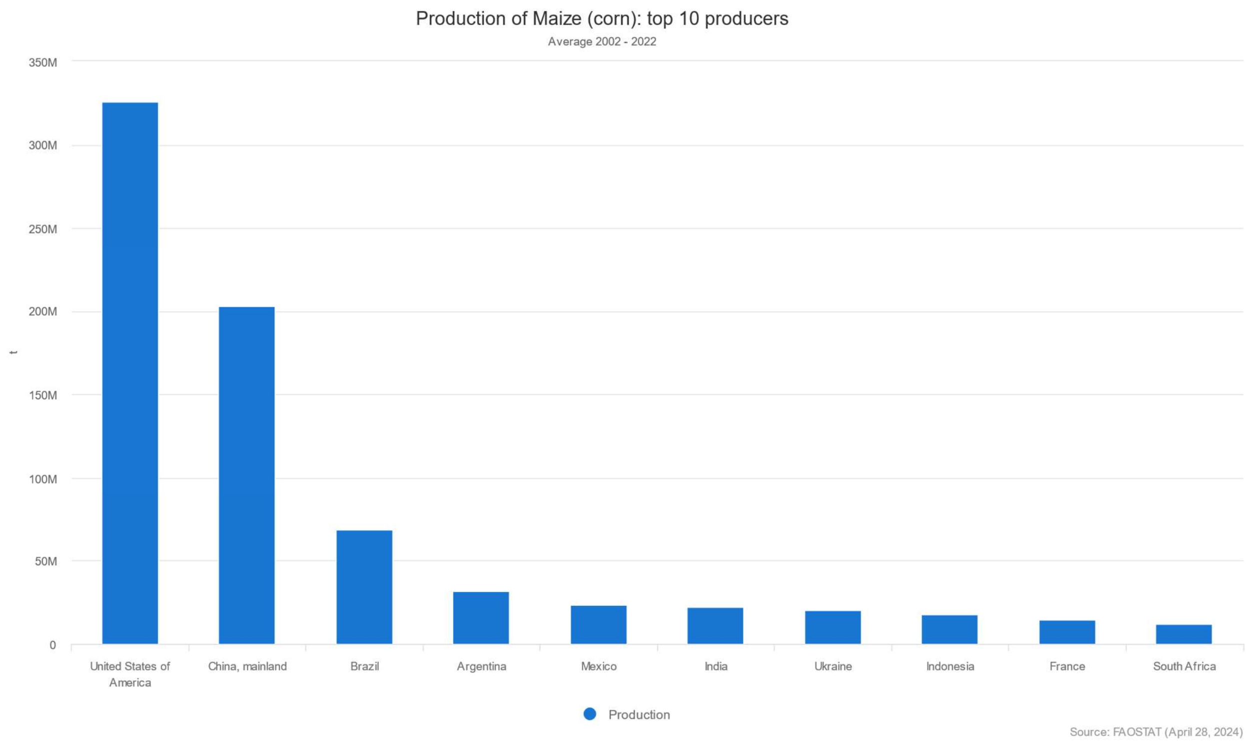

Figure 3: Top producer of maize Source: (FAOSTAT 2024)

2.2. Overview of photosynthesis under abiotic stresses

Many physiological, biochemical, and molecular mechanisms regulate plant growth, but one important metabolic process that significantly influences plant growth and development is photosynthesis. In actuality, the chemical energy required for several metabolic functions comes from the process of photosynthesis, which transforms light energy into a chemical form that may be used. This essential mechanism is present in all green plants, and it may be found in photosynthetic bacteria as well as in seas and on land. The term photosynthesis literally means "synthesis using light." In precise terms, light energy is responsible for the production of oxygen and the synthesis of carbohydrates from carbon dioxide and water (Pan et al. 2012; Taiz et al. 2014).

$$6\,CO_2 + 6\,H_2O \rightarrow C_6H_{12}O_6 + 6\,O_2$$

But in most plants, stressful conditions like drought, salinity, and unfavorable temperatures significantly impair photosynthesis by changing the organelles' ultrastructure, the concentration of different pigments and metabolites, including enzymes that are involved in the process, and stomatal regulation (Ashraf and Harris 2013).

Two essential steps in the process of photosynthesis are required: light reactions, which release oxygen and convert light energy into ATP and NADPH, and carbon reactions, which use the ATP and NADPH from the light reactions to fix CO_2 into carbohydrates (Fig. 4) (Dulai et al. 2011; Taiz et al. 2014).

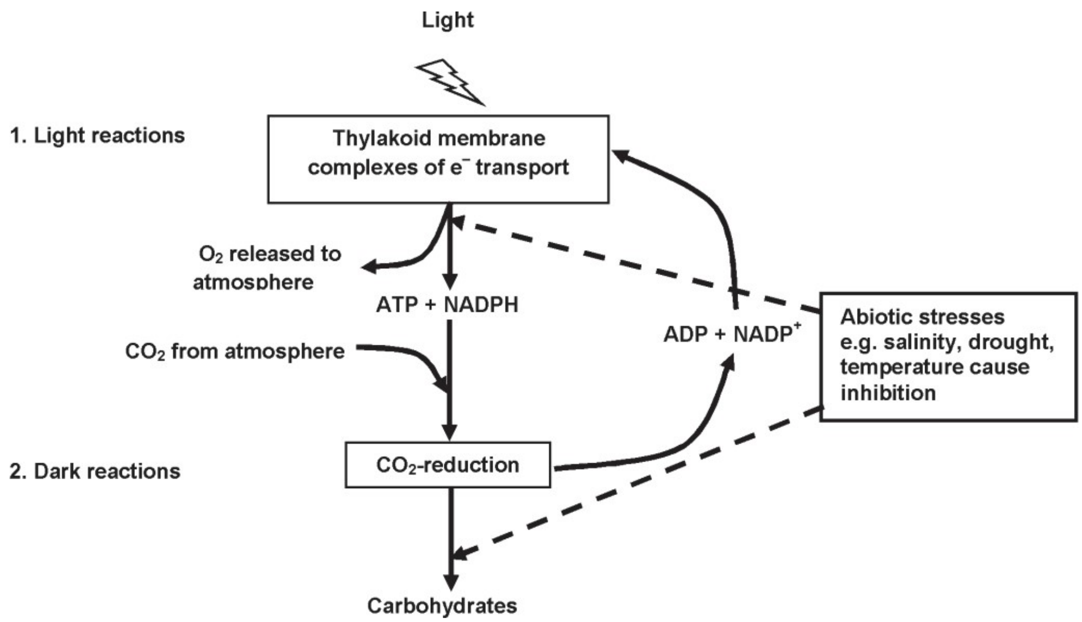

Figure 4: Light and carbon reactions of photosynthesis. Source: (Bhattacharya 2022).

The two primary pathways for CO_2 fixation are C3 and C4. Plants are classified as C3, C4, or C3-C4 intermediate based on the spatial arrangement of these pathways within leaf tissues, or as crassulacean acid metabolism (CAM) plants based on their temporal distribution (Doubnerová and Ryšlavá 2011; Freschi and Mercier 2012). Different photosynthetic systems allow plants to be adapted to different climate zones. For instance, C3 plants, which make up more than 95% of all plant species on Earth, grow well in cold, humid areas with low light intensity. C4 plants, on the other hand, grow in hot, arid climates with generally high light levels. Due to their better water-use efficiency (WUE) than C3 plants, C4 and CAM plants are typically the most suited to arid environments. They contain an extra carbon fixation pathway and unique morphology that limits photorespiration, therefore C4 plants have higher photosynthetic efficiency than C3 plants, notably in arid, hot, and high-light environments. Additionally, by closing their stomata throughout the day, CAM plants can efficiently conserve water and metabolic energy in difficult environmental situations (Taiz et al. 2014).

It has demonstrated that plants growing in regions with higher atmospheric CO_2 concentration are

less affected by drought and maintain a notable growth rate as compared to plants surviving lower CO_2 (Niinemets 2010). Elevated CO_2 concentrations have been observed to accelerate the growth and development of rice, a C3 species, resulting in increased crop output and modified grain composition. On the other hand, it has also been observed that the elevated CO_2 levels shorten the growing season and reduce yield in maize, a C4 plant. Hence, it appears that increased CO_2 concentrations mainly benefit C3 plants in terms of photosynthetic activity, while C4 plants benefit relatively less in terms of plant productivity (Kim et al. 2007). As a C4 crop, maize's water-use efficiency is indirectly increased by reduced stomatal conductance and transpiration, which leads to a somewhat higher rate of plant growth than a direct drift in photosynthesis. Since corn plants are already operating at almost full retaining photosynthetic capacity, they do not immediately benefit from CO_2 fertilization effects. Since maize is a summer crop and is expected to experience more frequent drought episodes, better water use efficiency may help the crop's vegetative growth. Abiotic stresses, however, have comparatively bigger effects on the plant's reproductive processes, therefore negative physiological costs under warmer temperatures may not be compensated by such a benefit (Hatfield 2016). Climate-resilient maize has been bred for better defensive qualities, yield potential, and consumer-favorite features, together with a remarkable resilience to stress conditions associated with a changing climate, in an effort to overcome the harmful situation (Hansen et al. 2019).

Various activities connected to growth and development rely on the interaction between intracellular organelles. The chloroplast, where both the light and dark reactions of photosynthesis occur, is the essential location for photosynthesis. This organelle is crucial in the regulation of stress responses, yet it is extremely susceptible to a variety of stressful conditions, including salt, drought, temperature extremes, flooding, fluctuating light intensity, and UV radiation (Biswal et al. 2008; Saravanavel et al. 2011). All these stresses cause stomatal or nonstomatal restrictions that lower the photosynthetic rate (Saibo et al. 2008; Rahnama et al. 2010). For instance, most green plants' stomatal conductance and leaf photosynthesis can be inhibited by drought stress, especially when it is mild (MEDRANO et al. 2002). Several studies have demonstrated that during the early phases of drought stress, stomata typically close resulting in increased WUE (net CO_2 assimilation rate/transpiration). It is well known that stomata closure inhibits water transpiration more than CO_2 diffusion into leaf tissues (Chaves et al. 2008; Sikuku et al. 2010). On the other hand, dehydration of mesophyll cells occurs under extreme drought stress, which results in a notable suppression of the fundamental metabolic processes of photosynthesis and a decrease in plant WUE (Anjum et al. 2011; Damayanthi et al. 2011). Mesophyll cells' ability to use the available CO_2 is reduced under drought stress (Karaba et al. 2007; Dias and Bruggemann 2010).

2.3. Plant response mechanism to different abiotic stresses

There are many different abiotic stressors that plants may encounter. According to the evolutionary perspective, organisms that have developed the ability to modify various defense-related response mechanisms to survive these shocks and return to normal basal metabolism are considered adapted. These environmental factors greatly limit production of crops and growth. For instance, an increase in atmospheric CO_2 may change the rate at which plants photosynthesize, resulting in variations in growth rate that often have a beneficial effect on biomass overall but a negative influence on nutritional quality (Obidiegwu et al. 2015). Stress-related stimuli generate unique changes in the physiology and growth of plants. Several mechanisms, including lipid signaling, transposable elements, photosynthesis and gas exchange, cell death, modifications in the composition of cell walls, nutrient translocation, transcriptional activity of genes, and antioxidant profile, can be altered during stress (Tenhaken 2015; Menezes-Silva et al. 2017; Bryant et al. 2021).

The physiological response mechanism to abiotic stresses consists of a complicated chain of events that starts with the perception of stress and culminates in a range of physiological, metabolic, and developmental reactions (Bhargava and Sawant 2013). All of these are summarized in the following (Fig. 5).

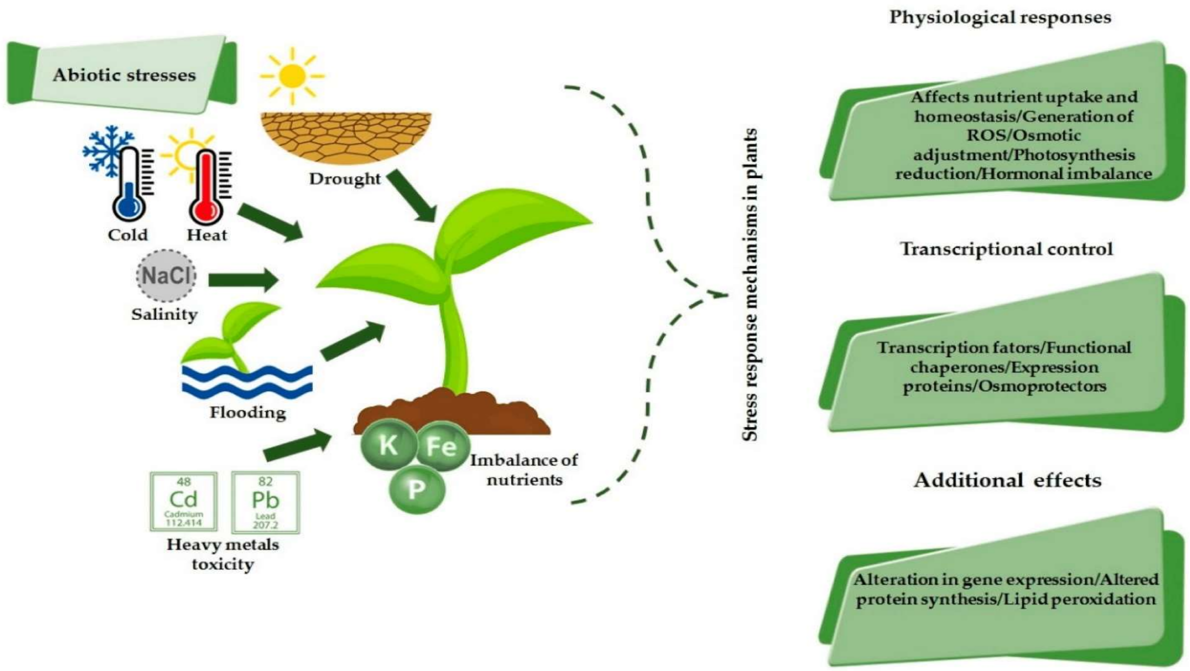

Figure 5: Plant reaction cascade to various abiotic stresses. Source: (dos Santos et al. 2022)**.**

When plants perceive these imbalances caused by the abiotic stresses listed above, they direct their resources and energy toward defensive mechanisms and procreation. Growth is slowed as a result, reducing the amount of biomass produced.

2.4. Drought stress

From an agricultural perspective, a drought is characterized by below-average precipitation, fewer rainy days, or above-normal evaporation, which frequently leads to a decline in crop growth and production (Rollins et al. 2013). The occurrence and distribution of rainfall, evaporative needs, and soil moisture-storing capacity are only a few of many factors that affect how severe a drought will be (Hayes et al. 2011).

Plant growth, yield, water relations, membrane integrity, pigment content, and photosynthesis are all impacted by drought (Manavalan et al. 2009). It is distinguished by a reduction in cell enlargement and growth, a decrease in stomata closure, a decrease in leaf water potential and pressure potential, and a decrease in water content (Anjum et al. 2011). By interfering with a number of physiological and biochemical functions, including photosynthesis, respiration, translocation, ion uptake, sugar and nutrient metabolism, and phytohormone production, it slows down the growth of plants (Farooq et al. 2009). A severe drought may cause photosynthesis to stop and metabolism to become disrupted, ultimately resulting in plant death (Jaleel et al. 2008). However, a plant's sensitivity to drought varies depending on its species, developmental stage, and the intensity and duration of stress (Demirevska et al. 2009). Drought resistance in plants has been assessed using a range of drought-related features, such as root and leaf attributes, osmotic adjustment capacities, water potential, abscisic acid (ABA) concentration, and cell membrane stability. Significant progress has been achieved in drought avoidance and tolerance over the past ten years as scientists have studied the genetic and molecular mechanisms of drought resistance to increase it in a variety of crops (Ha et al. 2012).

2.4.1. Plant response mechanism to drought stress

Plants experience drought as a multifaceted stress that impacts them at several levels of their organization, ranging from phenological and morphological to molecular (Anjum et al. 2011). When there is a significant water deficiency, the supply of water to the elongating cells is interrupted, which inhibits cell elongation. Important factors that affect plant water relations include relative water content (RWC), leaf water potential, stomatal conductance, rate of transpiration, leaf temperature, and canopy temperature. In many plant species, a reduction in the RWC in response to drought stress is frequently seen (Ings et al. 2013). When the amount of water in the soil is restricted, plant growth is usually hampered more in the shoots than in the roots. In certain situations, however, the ratio of biomass in the roots to shoots of plants in drying soil may even rise in comparison to that of well-watered controls (Anithakumari et al. 2012). The reduction of photosynthesis and suppression of leaf expansion during drought stress results in a decrease in leaf area (Avramova et al. 2015). Additionally, it results in decreased growth by impairing cell elongation, expansion, and mitosis (Potopová et al. 2015). Water shortages cause crop plants' yield traits to drastically fall. This is most likely caused by changes in leaf gas exchange brought on by stomata closure, phloem loading, assimilate translocation, and dry matter partitioning (Farooq et al. 2009; Anjum et al. 2011).

Drought is associated with alterations in leaf architecture and ultrastructure in most plant species (Rollins et al. 2013). The size of the leaves generally shrinks, stomata become fewer, stomata submerge in xerophytes and succulent plants, leaf cell walls thicken, the leaf surface becomes cutinized, the conductive system under develops, but there are more large xylem vessels, cereal leaves roll, and early senescence is induced (Anjum et al. 2011). Another characteristic that lowers transpiration and preserves water content in dry conditions is gloucousness (the presence of a bluish or grayish waxy coating on the surfaces of leaves, stems, or fruits that help to minimize the water loss by limiting transpiration (Farooq et al. 2009).

2.5. Heat stress

Crops may soon face difficulties in sustaining their development, growth, reproduction, and output due to global warming. Plants have developed a number of defense mechanisms, such as chemical reactions and modifications to their physiology and biochemistry, to try to lessen the impacts of heat stress and protect against the harm that comes with rising temperatures (Qu et al. 2013). Plants experience heat stress in the following situations: (i) high air temperatures, in which case they absorb energy from sensible heat transfer; (ii) solar radiation incident on the soil surface raises the temperature above the air temperature; and (iii) substantial heating in leaves, which can result in leaves heating very quickly (up to 15 °C above air temperature) due to solar radiation and inability to dissipate heat. Therefore, leaves with low transpiration rates are frequently exposed to high temperatures (Singsaas et al. 1999). Thermal stress can seriously harm the structure of proteins and the cell membrane, which produces reactive oxygen species (ROS) and oxidative stress. Furthermore, heat stress reduced the production of antioxidants and phytohormones, altered the arrangement of cell structures that affected hormonal homeostasis, and lowered the synthesis, transcription, and translation of heat shock proteins (HSPs) (Li et al. 2021).

2.5.1. Plant response mechanism to heat stress

By expanding their root systems, reducing their stomata and conductance, and curving, folding, and shrinking their leaf surfaces to lessen water loss through evapotranspiration, plants modify their morphology to endure heat stress (Sicher et al. 2012). Abiotic factors like drought and high temperatures affect the growth and development of many plants, reducing the production of crops. Heat stress disrupts plants in many ways, changing membrane and protein stability, disrupting protein and nucleic acid metabolism, deteriorating membrane structure, and preventing photosynthesis, to name a few negative consequences (dos Santos et al. 2022). All of these are summarized in (Fig. 6).

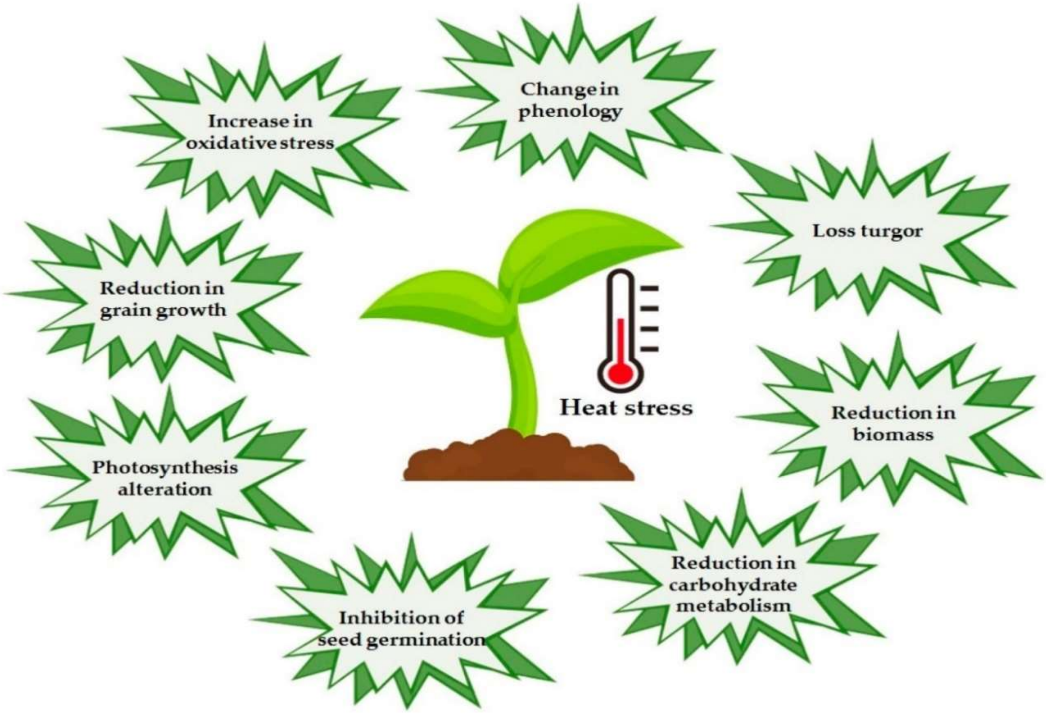

Figure 6: A few consequences of heat stress on plants. Source:(dos Santos et al. 2022).

Plants undergo physiological changes as a result of heat stress. Plant development is impeded when the photosynthetic machinery is disrupted, which lowers transpiration because of stomatal closure and CO_2 concentration, inhibits the rates of photosynthetic enzymes and ATP synthases, reduces leaf expansion, and speeds up senescence (Wahid 2007; Farooq et al. 2009). In order to alleviate heat stress, plants remobilize their starch reserve in chloroplasts by releasing sugars, energy, and derived metabolites that help them survive stressful times and avoid more damage. This is done by altering the metabolism of carbon assimilation (Raza 2022).

2.6. Remote sensing

Remote sensing (RS) is the study of identifying features on the earth's surface and estimating their geo-biophysical characteristics through the use of electromagnetic radiation as a medium. Spectral, spatial, temporal and polarization signatures are key features of the sensor/target, which facilitate target discrimination. Before spectral information is extracted, the earth surface data as perceived by the sensors at various wavelengths (reflected, scattered, and/or emitted) is adjusted geometrically and radiometrically (Navalgund et al. 2007).

Agricultural remote sensing is a very helpful technique that enables synoptic, remote, and non-destructive large-scale crop observation. A sensor installed on a platform which could be a field robot, remotely piloted aircraft (RPA), satellite, or unmanned aerial vehicles (UAV) is typically involved. The sensor gathers electromagnetic radiation from plants, either reflected or emitted, and processes it further to create products and information that are useful. This data includes the characteristics of the agricultural system and how they change across time and space. Functional traits are the biochemical, morphological, phenological, physiological, and structural physiognomies that control the fitness or performance of an organism (plant). RS effectively establishes a relationship between plant radiance and the corresponding characteristics to extract valuable information, such as the soil moisture content, chlorophyll content, and leaf area index (LAI). Accurate information from RS products, however, requires knowledge of several aspects, including crop phenological stage, crop type, soil type, location, wind speed, precipitation, humidity, sun radiation, nutrients availability, etc (Weiss et al. 2020).

In agricultural studies, multispectral pictures (e.g., Landsat, Sentinel 2, and SPOT images) have been utilized extensively to retrieve a variety of crop and soil variables, including yield, biomass, soil degradation, and crop chlorophyll content (Jr. and Daughtry 2018). However, the accuracy of the variables that are retrieved is frequently limited due to the limitations in spectral resolution, and early indicators of crop stressors (such as crop disease or nutrient deficit) cannot be efficiently and promptly detected (Adão et al. 2017). With hundreds of bands, hyperspectral images (such Hyperion, CASI, and Headwall Micro-Hyperspec) can record more detailed spectral responses, making them better equipped to identify minute changes in ground covers and how they change over time. In order to overcome the aforementioned difficulties and enable quicker and more precise identification of crop physiological condition, hyperspectral imagery can be employed (Lucieer et al. 2014).

Vegetation indices are frequently used to estimate vegetation and crop factors using NIR (near infrared) and visible regions of the electromagnetic spectrum. Healthy plants usually exhibit extremely low reflectance and transmittance in visible regions and very high reflectance and transmittance in NIR (near infrared). Photosynthetic and accessory pigments in the visible range had a strong absorptance, whereas subcellular particles or pigments had a low absorptance. Additionally, there was significant scattering at mesophyll cell wall interfaces in the near-infrared region (Slaton et al. 2001).

2.6.1. Stress effects

Facts	References
The rate of transpiration increased gradually with leaf temperature, suggesting that inhibition was not linked to stomatal closure. At leaf temperatures above 38°C, net photosynthesis (P_n) was inhibited, and the inhibition was significantly more pronounced when the temperature increased rapidly rather than gradually.	(Crafts-Brandner and Salvucci 2002)
Various parameters like membrane stability, chlorophyll fluorescence, and chlorophyll concentration all significantly decreased in sensitive genotypes during prolonged heat stress and abrupt heat shock, indicating their vulnerability to high temperatures. On the other hand, heat-tolerant genotypes showed a lower effect on these parameters, which may be related to reduced damage from oxidative stress.	(Yadav et al. 2018)
The formation of dry matter was hindered by high temperatures, drought, and their combined stress at various phases, which increased leaf senescence and reduced summer maize's photosynthetic ability.	(Hu et al. 2023)
This study showed that, in plants under drought stress, there was a considerable decrease in the F_v/F_m, PI, and RWC values.	(Badr et al. 2020)
When they grew maize in an N-deficient situation, they observed a significant decrease in the amount of chlorophyll in the leaves, as well as in the concentrations of soluble protein and N, Leaf area index (LAI), CAP, P_n, and the dynamic activities of PEPC and Rubisco. These decreases were also linked to leaf senescence.	(Wei et al. 2016)

3. Materials and Methods

3.1. Germination of Maize

The experiment was conducted at laboratory of plant physiology and plant ecology of Hungarian University of Agriculture and Life Sciences, Gödöllő Hungary. We germinated a series of maize in a tray containing 24 plants on 15th August 2023. After 3 weeks maize seedlings were grown in jars containing nutrient solutions, based on modified Hoagland's solution (Taiz et al. 2014). These nutrient solutions contain all the macro, meso, and micronutrients important for germination of plants. Out of these 24 plants, 12 plants were grown in Full nitrogen solution and 12 in Nitrogen deficient (10% of nitrogen solution) (Fig. 7).

Figure 7: Plants were grown in jars containing solutions with all necessary nutrients

The nutrient solutions had to be changed every week. All plants were kept under the same ambient temperature and humidity for five weeks (Fig. 8). On the 5th Monday a set of measurements had to be performed and at that time plants were subjected to stress treatment. We faced a problem with pH during preparation of solution, so added acetic acid to lower the pH to 6.5.

Figure 8: Seedlings of maize in the plant growth chamber

3.2. Treatments

The following treatments were done on plants:

12 Full: 7 Control, 2 Drought and 3 combined (Heat+Drought).
12 N10: same as Full

On the 5th week setting stress treatments:

- **Control**: no stress (Plants remained in the same place untreated)
- **Drought stress:** It was achieved by adding Polyethylene glycol (PEG-6000) to the nutrient's solutions (87.5g/0.7l)
- **Heat stress:** Prior to the second set of measurements, the plants were kept in a separate growing chamber and exposed to severe heat stress for 3 days as shown in (Fig. 9).

Figure 9: Plant was kept in chamber to subject heat stress

We performed the measurements twice for both series of maize in the laboratory.

- first set of measurements at the start of the 5th week to define the non-stressed state of the plants (before stress).
- second set of measurements at the start of the 6th week to see how plants react to stress treatments (after stress).

3.3. Measurements

3.3.1. Measuring photosynthetic performance

Photosynthetic activity (PN, µmol CO_2 m^{-2} s^{-1}) and transpiration rate (TR, mmol H_2O $m^{-2}s^{-1}$) of the fully developed leaves were measured by a portable photosynthesis system CIRAS-2 infrared gas analyzer (PP Systems, USA) as shown in (Fig. 10). Before starting the measurements, we checked the color of the adsorbents, connected the battery with an extra light source and changed the CO_2 cartridge.

Figure 10: Measuring photosynthesis and other parameters using PP-system

We placed the 3rd leaf of each plant inside the leaf cuvette to measure the photosynthetic performance for a 5-10 min period until saturation intensity. By doing this we estimated carbon sequestration:

- at constant light intensity
- varied light intensity

We also calculated the light curve response of photosynthesis for different treatments. For this, we used the Michaelis-Menten equation,

$$\mathbf{P_n = \frac{\alpha.\ P_m\ .PAR}{\alpha.\ PAR\ +\ P_m} -\ Rd}$$

In the above-mentioned equation, **α** is the photochemical efficiency of photosynthesis at low light, $\mathbf{P_m}$ is the maximum rate of photosynthesis, **PAR** is the photosynthetically active radiation, and **Rd** is the rate of dark respiration.

3.3.2. Measuring reflectance

A Qmini (RGB Photonics, Germany) spectrometer was used for reflectance measurements. We measured reflectance at the 3rd leaf of each plant. It was important for calculating the Vegetation Indices (VIs) for example PSRI, PRI, and mNDVI (Table 1). The dark reference (noise) was subtracted from the spectra recorded in the middle of the 3rd leaf of each plant and this value was then divided by the reflectance from the white reference. VIs was calculated as follows:

Table 1: Vegetation indices applied that are linked to vegetation status: chlorophyll content, leaf fluorescence, and stress effects (R corresponds to the noise and white surface corrected reflectance).

Abbreviation	Vegetation Index	Formula	Applications	References
PSRI	Plant senescence reflectance index	$\frac{(R_{680} - R_{500})}{(R_{750})}$	Carotenoid/chlorophyll ratio	(Merzlyak et al. 1999)
PRI	Photochemical reflectance index	$\frac{(R_{531} - R_{570})}{(R_{531} + R_{570})}$	Reliable water-stress index	(F. Thenot and Winkel 2002)
$mNDVI_{705}$	Modified red edge Normalized Difference Vegetation Index	$\frac{(R_{750} - R_{705})}{(R_{750} + R_{705} - 2 * R_{445})}$	Vegetation greenness and stress detection	(Li and Guo 2018)

3.3.3. Estimation of pigment content

We used a portable device Konica Minolta SPAD 502 (Osaka, Japan) for estimation of pigment content (chlorophyll) in leaf. A quick and non-destructive method was used for chlorophyll content estimations in the 3rd leaf of each plant. Before taking the measurements, we made calibration of device and took three measurements on the same 3rd leaf of each plant with equal interval of distance and then pressed the average button to calculate the mean value (Fig. 11).

Figure 11: Measuring pigment content by using SPAD

3.3.4. Measuring fluorescence signal

We used FluorPen that is a battery-operated, portable fluorometer that allows for the rapid and accurate measurement of chlorophyll fluorescence parameters in the field, greenhouse, or laboratory. It can be used to test herbicides, monitor photosynthetic activity, detect stress, or screen for mutants. FP 100-MAX-LM includes all features of the FluorPen FP 100-MAX, i.e., it measures chlorophyll fluorescence parameters Ft, QY, NPQ, OJIP, and Light Curve (QY).

We placed the plants in 20 minutes of dark adaptation and took measurement from the 3rd leaf of each plant with running light curve (LC) program (Fig. 12).

Figure 12: Measuring chlorophyll fluorescence by using Fluorpen

3.3.2. Measuring biomass

After the second measurement we measured the biomass, for this each plant was cut at the root collar/crown and the Above-Ground Biomass (AGB) and Below-Ground Biomass (BGB) were separated.

- Measured the fresh weight of both AGB and BGB
- After drying the samples to constant weight (80°C, ~3days), the dry mass was measured.

From these values, the moisture content was determined by their difference.

3.4. Statistical analysis

Microsoft Excel 2013 (Microsoft, Redmond, WA, USA) was used for processing data and plotting graphs between measured variables. The solver function of MS Excel was used for fitting non-linear model (Michaelis-Menten model) on measured light curves. To compare the different datasets in the form of boxplots, we used R-software (R Core Team) and later their comparison groups were tested by one-way ANOVA.

4. Results and Discussions

4.1. Light curve response of photosynthesis for different treatment plants

Table 2 contains the variables (model parameters) obtained after fitting the Michaelis-Menten model in solver on dataset of the photosynthetic activity as a function of photosynthetically active radiation (PAR).

Table 2: Measured variables of Michaelis-Menten equation for different treatment plants

Treatments	**photochemical efficiency of photosynthesis at low light (α)**	**maximum rate of photosynthesis (P_m)**	**rate of dark respiration (Rd)**
Full N (Control)	0.0443	19.3263	0.52
N10 (Control)	0.0567	15.0391	0.95
Full N (Heat+Drought)	0.0094	0.45857	0.38
N10 (Heat+Drought)	0.0041	2.01	1.40

We found a significant difference among the 4 different treatments how they respond to light curve. The following graph (Fig. 13) shows that the controlled plants grown in full nutrient (Full N) and deficient nutrient solution (N10) showed much higher photosynthetic activity as compared to stressed plants. It was observed that the rate of photosynthetic activity increases with increasing photosynthetically active radiation (PAR). In the set of both (Full N and N10) stressed plants, photosynthetic activity is affected by heat and drought. They also showed more respiration at low photosynthetically active radiation (PAR), whereas in controlled treatments it was not so significant. Overall, the rate of photosynthetically activity decreases when plants are grown in nutrient deficient solution and under stressed conditions (heat and drought). This shows that nitrogen fertilization can help plants maintain their photosynthetic capability and better withstand drought stress.

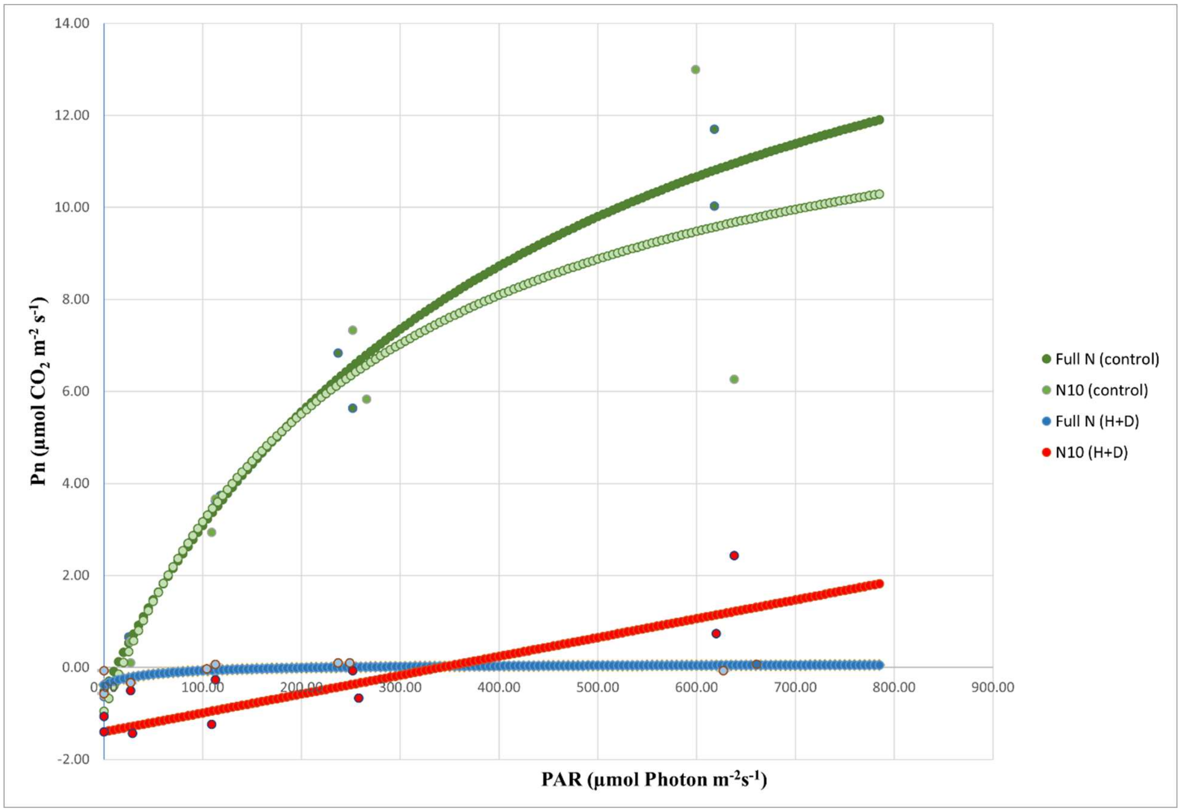

Figure 13: Light curve response of net photosynthesis under different treatments

4.2. Correlation between measured variables

4.2.1. Between P_n and TR

The correlation between net photosynthesis (P_n) and transpiration rate (TR) in maize is generally positive under optimal conditions as shown in (Fig. 14), but it can be affected by several environmental factors like heat and drought stress. Stomatal openings control both transpiration and photosynthesis. Water vapor is also lost as stomata open to let CO_2 in for photosynthesis. Consequently, higher transpiration rates are frequently associated with enhanced photosynthetic activity. The regression equation between net photosynthesis (P_n) and transpiration rate (TR) was **y=0.0682x+0.0902** and its correlation coefficient was **R^2 = 0.9232** with positive linear relationship.

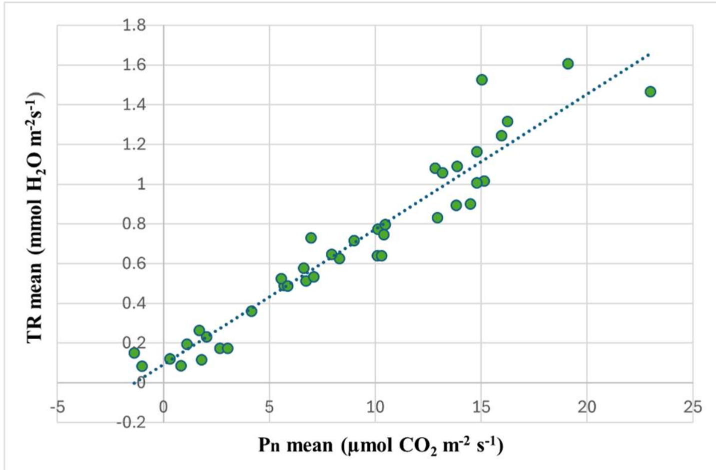

Figure 14: Correlation between P_n and TR

4.2.2. Between SPAD value and mNDVI

Modified red edge Normalized Difference Vegetation Index (mNDVI) analyzes the reflectance of particular light wavelengths using remote sensing data to evaluate the general health of the vegetation. Higher value of mNDVI indicates denser and healthier vegetation. Greater mNDVI values are typically correlated with greater SPAD values (Fig. 15). More chlorophyll in maize plants causes them to absorb more light in the red spectrum and reflect more in the near-infrared spectrum, leading to higher mNDVI values. We found the regression equation between SPAD value and mNDVI was **$y = 56.275x - 3.1915$** and its correlation coefficient was **$R^2 = 0.705$** with positive linear relationship. Our result is in agreement (Taifeng and Huffman 2015; Yadav et al. 2018) with proving that chlorophyll content of the leaves could be estimated well by remote sensing approach.

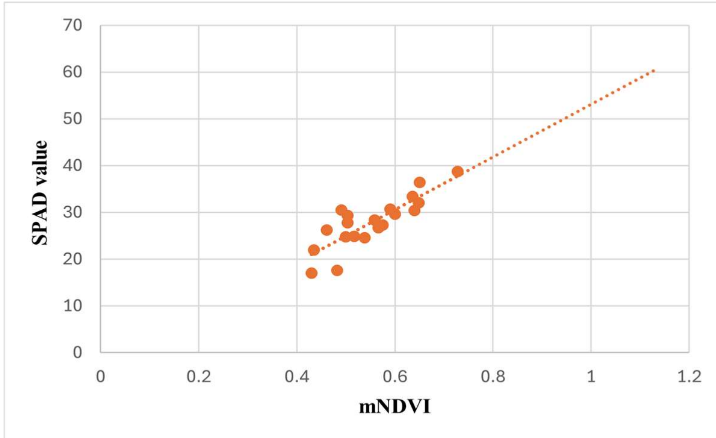

Figure 15: Correlation between mNDVI and SPAD value

4.2.3. Between PRI and F_m

The correlation between maximum fluorescence (F_m) and photochemical reflectance index (PRI) is crucial for determining photosynthetic efficiency and plant health (Fig. 16). We found the positive relationship between PRI and F_m. Both PRI and F_m often exhibit greater values when plants are healthy and actively photosynthesizing. Because of changes in pigment composition and light-harvesting efficiency, PRI levels may drop under stressful conditions (such as drought or nutrient deficiencies), and F_m may also drop, indicating a fall in photosynthetic efficiency. The regression equation between SPAD value and F_m was **y = 6E-05x + 0.0007** and its correlation coefficient was **R^2 = 0.3052** with positive linear relationship.

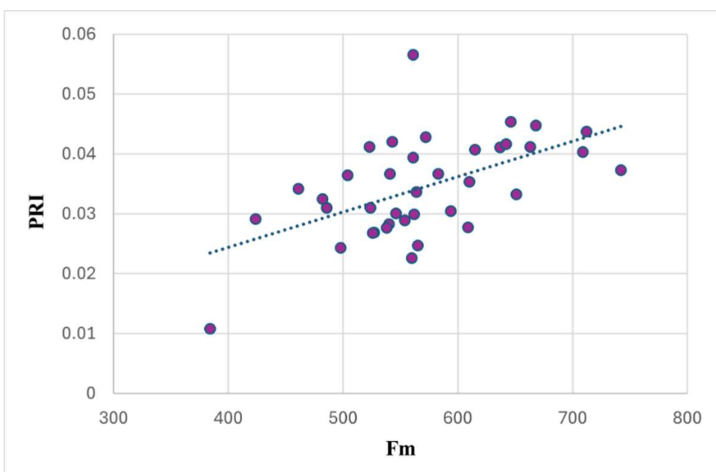

Figure 16: Correlation between F_m and PRI

4.2.4. Between water content and TR

In plants, transpiration rate and water content have a usually positive relationship, which means that when water content falls, transpiration rates may correspondingly decrease as shown in (Fig. 17). While a sufficient amount of water encourages increased rates of transpiration, water stress can result in lower rates, which can affect the growth and health of plants. We found the regression equation between water content and transpiration rate (TR) was **$y = 0.0351x - 2.4616$** and its correlation coefficient was **$R^2 = 0.0833$.**

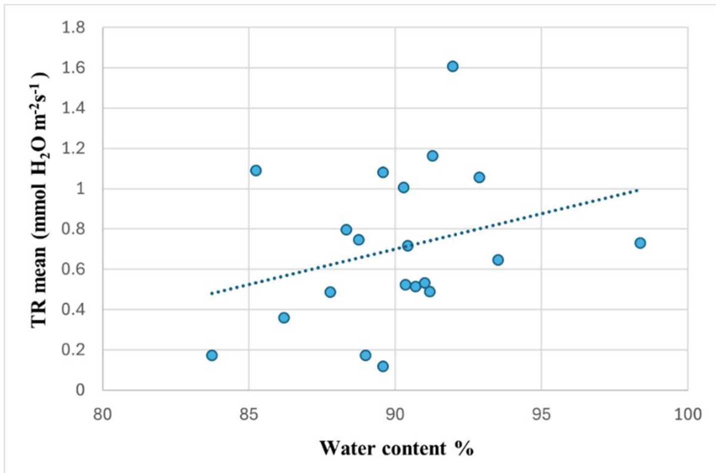

Figure 17: Correlation between water content and TR

4.3. Effects of the different treatments

We compared the measured variables against treatments and stress conditions and found noticeable differences.

4.3.1. Net photosynthesis (P_n) and treatment

The result in (Fig. 18) showed that the net photosynthetic value (P_n) value is significantly affected against full and deficient nutrient solution (N10) treatment and its statistical value is **($p = 0.0038076$)**. The mean P_n value in full treatment was 10.30 and in N10 was 6.96. It was found that the net P_n value in N10 treatment was 32.42% lesser than full treatment plants. The reasons could be inadequate nutrients availability in N10 solution can result in decreased biomass and leaf area, which further limiting the plant's capacity for efficient photosynthetic processes. Our finding is in accordance with (Wei et al. 2016).

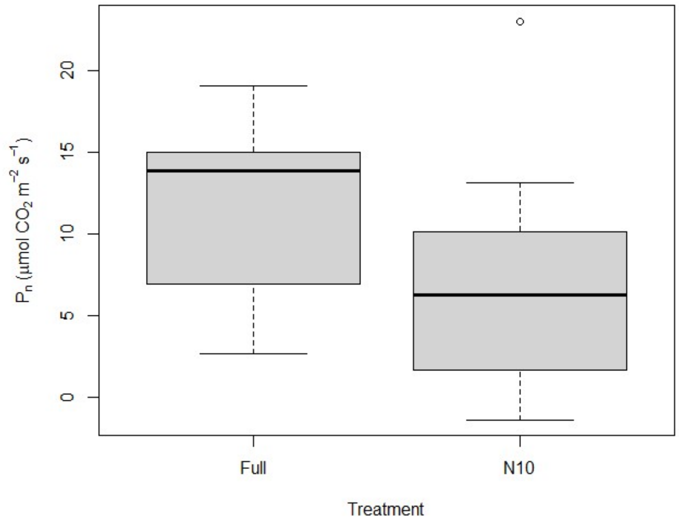

Figure 18: Comparison between net photosynthesis (P_n) and treatment

4.3.2. Shoot/root ratio and treatment

The result in the (Fig. 19) showed that the shoot/root ratio is higher in full nutrient solution as compared to N10 treatment, but the difference was not significant in ANOVA **(p= n.s).** A reduced shoot-to-root ratio is frequently the result of stunted shoot growth caused by nutrient deficiencies in a 10% nutrients solution. The reason could be plants may invest more in developing their roots in order to find the few nutrients available in the soil, which would result in a larger root mass than shoots. This may occur in reaction to nutrient shortage and stress.

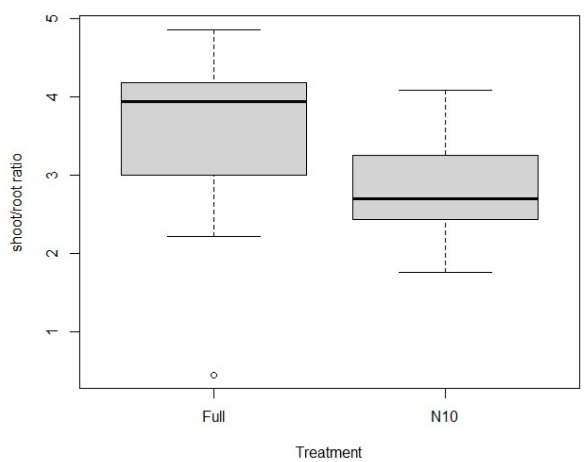

Figure 19: Comparison between shoot/root ratio and treatment

4.3.3. mNDVI and treatment

The results in (Fig. 20) showed the value of mNDVI is higher in full nutrient solution plant than N10 treatment and statistical value isn't significant in ANOVA **(p=n.s)**. The reason could be that the reduced chlorophyll content from inadequate nutrition can result in less efficient light absorption. The mNDVI is lowered as a result of this decrease in NIR reflectance and possible rise in red spectrum reflectance.

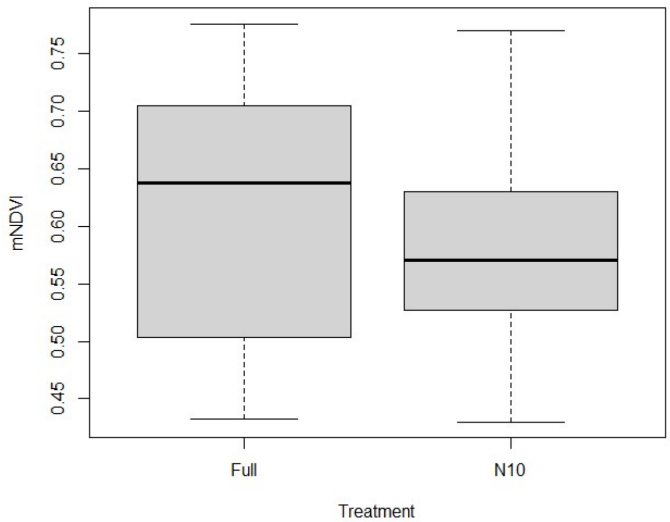

Figure 20: Comparison between mNDVI and treatment

4.3.4. Transpiration rate (TR) and stress

The result in the (Fig. 21) shows that the transpiration rate (TR) decreases significantly from control to stress situation and in statistical analysis we found the difference significant **(p= 0.00238)**. Normally, transpiration rates are high under control settings because there is an ideal supply of water. Transpiration rates sharply decline during drought stress when stomata close to conserve water. The impacts of heat stress and drought stress are compounded, causing the plant to experience more physiological stress and even lower transpiration rates. The productivity and health of plants may suffer significantly as a result.

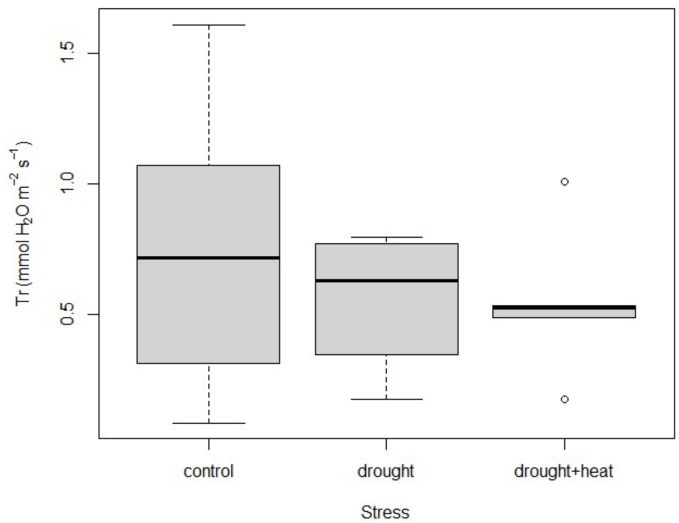

Figure 21: Comparison between transpiration rate and stress

4.3.5. Photochemical reflectance index (PRI) and stress

The result in the (Fig. 22) showed that control plants exhibit high PRI values, but heat, drought, and combination stress cause values to gradually decline, and statistical value isn't significant in ANOVA (p =n.s). As water availability declines, stomatal closure and stress-induced chlorophyll degradation may cause plants to have lower photosynthetic efficiency. Like drought stress, heat stress frequently causes a decrease in chlorophyll efficiency and content, which lowers PRI values.

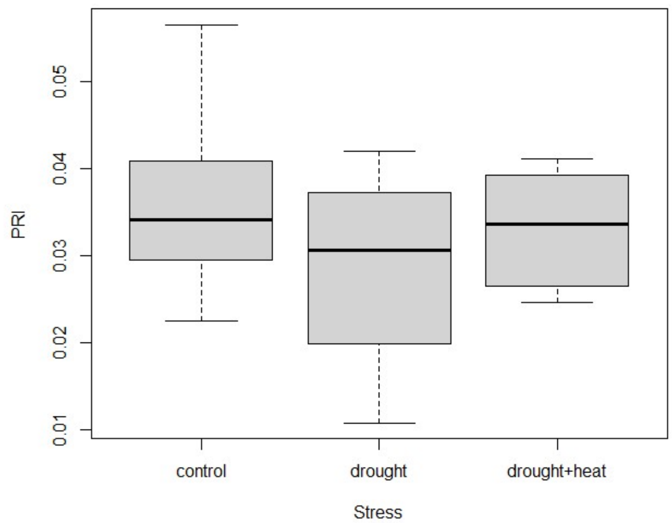

Figure 22: Comparison between PRI and stress

4.3.6. F_v/F_m and stress

The ratio F_v/F_m known as the maximum quantum efficiency of photosystem II (PSII), is a vital measure of photosynthetic performance and plant health. We found no significant between the control and stressed plants ($p>0.05$). However, the value of F_v/F_m was noticeably affected in stressful conditions as shown in (Fig. 23). Reduced photosynthetic efficiency results from stomatal closure brought on by reduced water availability, which restricts CO_2 uptake. This may result in a decreased F_v/F_m ratio and more photo-inhibition. Our results are in accordance with (Badr et al. 2020).

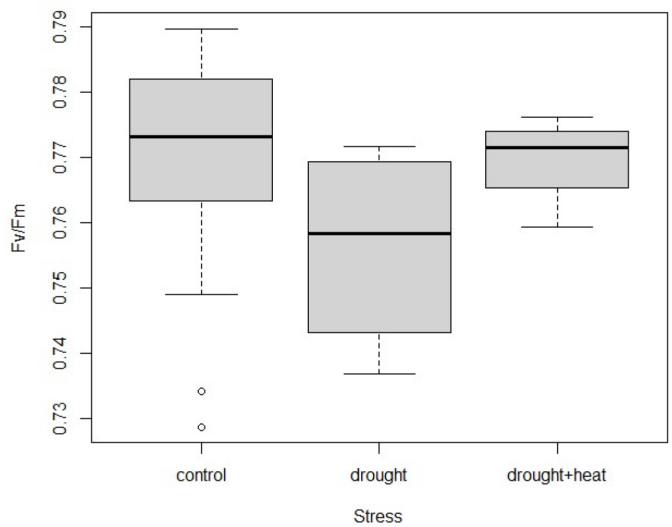

Figure 23: Comparison between F_v/F_m and stress

5. Conclusion and recommendations

This study highlights the importance of nutrient availability in regulating resilience by demonstrating the significant effects of abiotic stresses, particularly drought and combination heat-drought conditions, on maize's physiological performance. Maize, an essential global crop, faces increased productivity challenges due to these stresses, which can significantly reduce photosynthetic capacity and plant health. Measurements were taken to assess photosynthetic performance, water retention, chlorophyll content, and other physiological indicators using tools like the CIRAS-2 infrared gas analyzer and vegetation indices derived from remote sensing (e.g., PRI, mNDVI). Chlorophyll content, water content, photosynthetic performance, transpiration rate, and other physiological markers were measured using the CIRAS-2 infrared gas analyzer, remote sensing indices (e.g., PRI, mNDVI, PSRI), SPAD-502, and the Fluorpen.

This study shows that nitrogen availability is crucial for maintaining maize's photosynthetic performance under stress by analyzing both nutrient-sufficient (Full N) and nutrient-deficient (N10) treatments under control and stress conditions. Superior performance in light curve response studies demonstrated that maize plants grown with sufficient nitrogen had stronger photosynthetic activity even in challenging conditions. Conversely, under stress, nutrient-deficient plants showed decreased rates of dark respiration and photosynthetic efficiency, indicating that sufficient nitrogen fertilization can mitigate the negative impacts of abiotic stresses by preserving greater levels of photochemical efficiency.

The correlation between transpiration rate (TR) and net photosynthesis (Pn) highlights maize's response to changing environmental factors. The balanced function of stomatal openings in promoting CO_2 uptake and controlling water vapor loss was demonstrated by the positive correlation between photosynthesis and transpiration under ideal circumstances. However, under stress, this link weakened as plants closed their stomata more and more to conserve water, which limited the intake of CO_2 and thus decreased photosynthetic rates. This trade-off illustrates the plant's adaptation mechanism, which prioritizes water conservation above carbon accumulation when under prolonged stress. These reactions highlight the intricate decision-making processes of stressed plants and imply that water supply naturally restricts maize's physiological adaptability, particularly in situations of combined heat and drought stress.

In order to evaluate plant health and identify early indicators of stress, vegetation indices like the Modified Red Edge Normalized Difference Vegetation Index (mNDVI) and the Photochemical Reflectance Index (PRI) could be useful. Both indices - one of them representing chlorophyll content and the other one the photosynthetic efficiency, thus, the overall health of the plant - had a high positive connection with SPAD values. Full-nutrient plants tend to have higher mNDVI values, which are indicative of denser and healthier vegetation. Under heat-drought stress, the PRI also significantly decreased, suggesting a decrease in chlorophyll content and photosynthetic efficiency. This decrease under stress demonstrates the importance of vegetation indices in remotely monitoring stress responses and offering useful, non-destructive precision agriculture techniques.

Another crucial component of plant physiology under stress, the shoot-to-root ratio, was likewise strongly impacted by nutrient deficiency. In nutrient-deficient conditions, maize plants showed a reduced shoot-to-root ratio. This is probably an adaptation reaction meant to increase root biomass to aid in nutrient uptake. This change toward root development highlights how maize reallocates resources to improve its ability to absorb nutrients from the soil in response to nutrient scarcity.

Stressful conditions also had an impact on the Fv/Fm ratio, which measures the maximum quantum efficiency of Photosystem II (PSII). Although not statistically significant in all tests, observed decreases in this ratio corresponded to decreased CO_2 uptake as a result of stomatal closure. This decrease suggests heat and drought conditions cause photoinhibition, which further reduces photosynthetic efficiency beyond stomatal regulation. The study's insights into nutrient-stress dynamics present encouraging ways for improving maize sustainability and yield, highlighting the necessity of integrated strategies that incorporate adaptive crop management, real-time monitoring, and nutrient optimization in battle for world food security.

The following measures can be recommended:

- Optimized nitrogen fertilization is advised as part of maize production practices to increase resistance against heat stress and drought. Even in stressful situations, this strategy can assist in maintaining improved photosynthetic performance and water-use efficiency.
- Early identification of stress conditions in maize fields should be accomplished by the use of remote sensing techniques, particularly vegetation indices such as mNDVI and PRI. By taking a proactive approach, prompt action may be possible, maximizing resource utilization and maybe raising agricultural yields.

- Future research should examine other stress combinations since combined stress conditions, such as heat and drought, demonstrated a compounding effect on plant physiology. This can aid in developing strong plans for protecting crops from intricate environmental problems.
- Breeding initiatives to develop maize varieties with increased resistance to heat and drought are necessary because of the significant impact these conditions have on the photosynthetic and transpiration rates of maize. In areas where climatic fluctuation is becoming more pronounced, this will promote sustainable maize production.

6. Summary

This study investigates how maize plants react physiologically to different nutrient availability levels and stress conditions, especially heat and drought. Maize, an essential global crop, faces increasing challenges due to these abiotic stresses, which significantly affect growth, yield, and resistance. The experiment was conducted in a controlled environment, involved growing maize under full-nutrient solution and nitrogen-deficient, with selected plants subjected to drought, heat, or a combination of both these stresses.

Measurements were taken to assess photosynthetic performance, water retention, chlorophyll content, and other physiological indicators using tools like the CIRAS-2 infrared gas analyzer and remote sensing indices (e.g., PRI, mNDVI and PSRI). Chlorophyll content, water content, photosynthetic performance, transpiration rate, and other physiological markers were measured using the CIRAS-2 infrared gas analyzer, remote sensing indices (e.g., PRI, mNDVI, PSRI), SPAD-502, and the fluorpen.

The results showed that the availability of nitrogen is essential for maintaining photosynthetic adaptability and efficiency under stress. In comparison to nitrogen-deficient plants, full-nutrient plants exhibited greater photosynthetic rates, chlorophyll content, and improved water retention. A lower Fv/Fm ratio, which suggests decreased efficiency, indicates that the combined heat and drought treatment had a considerable impact on photosynthetic parameters. These findings demonstrate the value of proper nutrient management as well as the possibility of remote sensing indicators for early crop stress detection.

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8. List of Tables

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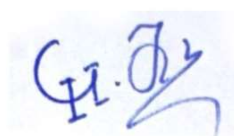

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