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Breeding for Early Heat Stress Tolerance in Wheat

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ABSTRACT

Wheat, a major contributor to global food security, is highly vulnerable to early heat stress, particularly as climate change intensifies. Early sowing practiced to optimize moisture and avoid terminal heat stress, exposes crops to elevated temperatures during critical stages like germination, tillering, and grain filling. As a C_3 plant, wheat thrives at 15-20°C, but early heat disrupts photosynthesis, reduce chlorophyll content, impair carbon partitioning, and negatively affect grain quality and yield. To combat these challenges, wheat exhibits various adaptive mechanisms, including improved membrane stability, enhanced photosynthesis, and activation of heat shock proteins (HSPs) that protect cellular components from heat damage. Breeding strategies should be adopted to mitigate early heat stress to sustain wheat production. Traditional breeding focuses on selecting resilient genotypes, while advanced techniques like genome-wide association studies (GWAS), marker-assisted selection, and CRISPR-Cas9 offer precise genetic improvements. Speed breeding further accelerates development of heat-tolerant varieties. Screening tools like Canopy Temperature Depression (CTD), Heat Susceptibility Index (HSI), and SPAD meter readings for chlorophyll content help identify tolerant genotypes. Integrating genomics, transcriptomics and metabolomics technologies enhances the understanding of heat tolerance mechanisms. Collaborative efforts among breeders, biotechnologists and agronomists are crucial for developing heat-resilient wheat, ensuring global food security amidst climate change.

Keywords: Wheat, early heat stress, heat tolerance, breeding strategies, heat shock proteins, CRISPR-Cas9

Introduction

Out of total world food grain production, wheat shares about 30% contribution. Wheat accounts for about fifty percent contribution in global grain market. Wheat demand is projected to be 840 million tonnes to feed around 10 billion people by 2050 (Sharma et al., 2015). The well-known constraint behind low production in wheat is global warming. Wheat being C_3 plant requires a range of 15-20^{O}C temperature conditions as compared to C_4 crop (Ruan et al*.*, 2012).

With global climate change, heat stress is becoming a more serious limitation on wheat production (Ni et al*.*, 2018). Majorly, abiotic stresses like heat causes more yield loss, compared to biotic factors (Coast et al., 2022). As global temperatures rise, heat stress, a regular risk to wheat in the subtropics, becomes more dangerous in regions that produce wheat (Ding et al., 2021).

Farmers tend to sow wheat in early October to utilize most of the moisture after harvesting of rice. It saves at least one irrigation of the season. Also, along with adoption of good agronomic practices, early sowing keeps terminal heat stress escaped. Wheat due to early sowing, is harvested till end of March to early April. Moreover, most of the present cultivars are not bred for early sowing conditions. That is the main reason why present cultivars in wheat mature early and are poor yielding. Cultivars for farmer's field are not well adapted to early sowing environments. The role of genes behind breeding cultivars of wheat suitable for early as well as mid-season planting conditions is unknown till date (Bhanja et al., 2021).

Characteristics of wheat environment:

Climate factors such as temperature, moisture, CO_2 levels, weather changes, and soil moisture deficiency would have an impact on agricultural productivity, either positively or negatively (Joshi and Kar, 2009). Deryng et al. (2014) elaborated effects of high CO_2 concentration and impact of ever-changing climate on wheat production. The threatening significant effects of climate change on dropping yield potential of wheat was reported by Tripathi et al. (2016). Wheat production is expected to decrease by 6% for every degree increase in temperature. Around 100 million hectares of global area of wheat is heat prone. This area lies in low lying latitude of earth (Braun et al., 2010). Heat stress is also becoming a serious problem in colder northern wheat-growing regions due to rising severity throughout heading to maturity (Liu et al., 2014). Eastern Gangetic plains, peninsular region and central regions are most susceptible heat prone areas in India (Singh et al., 2007, Joshi et al., 2007). Heat stress occurs typically due to rising canopy temperature, which is dependent on air and soil temperature, soil and canopy properties, and soil moisture loss. Joshi et al. (2007) found that reducing the 'cold time' in wheat also reduced yield.

Genetic variability for adaptation and survival under heat stress:

Previous studies have found that high temperatures generate a variety of morphological,physiological, molecular, biochemical and cellular changes in plants (Barnabás et al., 2008; Almeselmani et al., 2012). There is growing evidence that heat stress has a major detrimental influence on yield during the reproductive phases (Farooq et al., 2011; Balla et al., 2012; Semenov and Shewry 2011). Major impacts of elevated temperatures include pollen sterility and abortion, drop in dough quality, hampered grain filling, reduction in seed weight etc. (Hays et al., 2007; Altenbach et al., 2012). In nutshell, yield is compensated on account of reduction in grain number, advanced grain maturity, reduction in tiller number, plant height, etc. (Rahman et al., 2009; Zhang et al., 2010).

Great negative impacts of heat are observed during flowering and reproductive stage, of wheat (Djanaguiraman et al., 2020). It is reported that after anthesis, if temperature rises from normal range (15°C-20°C) to high temperatures (40°C-45°C) yield of wheat gets by reduced to about 23% of normal production (Fleitas et al., 2020). However, reactions are also affected by the duration of heat stress, as well as the pace at which temperature rises. Because of a process known as basal thermotolerance, plants may still grow at temperatures over the ideal range. Pretreatment of wheat genotypes to mild heat develop tolerance in wheat genotypes to high lethal temperatures. Usual practice of exposure to gradual increase in temperatures develops heat tolerance in wheat genotypes (Qin et al., 2008; Mittler et al., 2012).

Most sensitive stages in wheat affected by heat stress includes stages from flowering to grain filling (Farooq et al., 2011). Elevated temperatures degenerate tapetum, interfere meiosis (Sakata et al., 2000, Zinn et al., 2010), and biomass accumulation, which ultimately reduces the grain yield in wheat (Reynolds et al., 2007).

Anatomical/ growth stages and phenophases:

1- Seed germination coupled with Tillering stage:

Various factors influencing seed germination and tillering in wheat are triggered by elevated temperatures during germination stage in wheat. Seed germination and seed vigour are the most significant features for obtaining a better crop stand and greater yield, and seed germination is primarily dependent on temperature, with the temperature range for optimum germination varying depending on the crop species. The normal temperature range favourable for seed germination in wheat is 1-4°C. The percentage of germination goes on decreasing above the optimal range of temperature. Germination percentage increases as the temperature rises from the base to the ideal range, and declines as temperature rises over the optimum range. High temperatures (45°C) induced cell death and embryo damage in *Triticum aestivum* during the early stages of germination. High temperatures are unsuitable for wheat development and the establishment of new seedlings (Akter and Rafiqul, 2017). Essemine et al., (2010) studied that the temperature rise in night conditions drops germination percentage at higher rate as compared to diurnal temperatures.

2- Grain filling duration:

Heat stress, among other abiotic stresses, has a negative impact on plant chlorophyll and grain filling stage. During the mid anthesis phases, excessive temperatures influence fertilisation and seed set, reducing wheat yield (Ferris et al., 1998). High temperatures also causes ultra-structure changes in the aleurone layer, increasing stomatal density, closing stomata, shrinking cell size and a decrease in wheat flour quality (Zahra et al., 2021). High temperatures limit uptake of sucrose which reduces starch synthesis in endosperm. It leads to improper carbon partitioning in the wheat plant (Harris et al., 2023).

3- Flowering and panicle development:

High temperatures have a detrimental effect on wheat, reducing productivity and production. High temperatures reduce the number of grains and reduce the maximum production potential during the floral initiation and spikelet development stages (Janjua et al*.,* 2010). Challenged seedling growth and photosynthesis as a result of decreased activity of photosystem II was observed in elevated temperature conditions by Tewari and Tripathy (1998).

4- Photosynthesis, respiration, and developmental stages:

High temperature affects leaf appearance and elongation and shortens the length of leaf elongation. It also retards root development during the reproductive stage due to reduced carbon partitioning to roots (Batts et al*.,* 1998). High temperatures above 40°C have a negative impact on photosynthesis and reduce the solubility of O_2 and CO_2. As a result, the rate of photosynthesis is reduced, the rate of respiration is increased, and the level of CO_2 is higher than the level of O_2 (Wingler et al*.,* 2000). High temperatures directly affects the activity of ribulose-1, 5-bisphosphate carboxylase/oxygenase, Rubisco binding protein and Rubisco activase in wheat leaves (Prasad et al*.,* 2008). Mitochondrial respiration is extremely temperature sensitive. When the temperature rises beyond 50°C, the rate of respiration drops, resulting in the damage of the respiratory mechanism. Short-term drought conditions also reduce root and leaf respiration. Increased inflow of assimilates ensures higher respiration rate of seed, and ultimately reduces yield due to improper assimilate partitioning in elevated temperature conditions (Wardlaw et al*.,* 1980). According to Rehman et al. (2009), productivity in wheat gets reduced per degree rise in temperature in tropical, subtropical, desert and arid regions. Viable leaf area is reduced which in turn affects photosynthetic rate as well as water use efficiency of wheat under high temperature stress conditions (Castro et al., 2007). Schuster et al. (1990) discovered that the source and sink relationship is disturbed in this regard. Figure 1 shows the effect of temperature on various physiological processes and growth rate of plants (Fitter and Hay 2012).

5- Final yield:

High temperatures have an impact on both the supply and sink of assimilates, reducing crop output. Under high temperatures, leaf area and photosynthesis, as well as shoot and grain biomass, rapidly reduced (Shah and Paulsen, 2003). While, temperature elevating from 27-32°C at night, grain production decreases by 90% (Jalil et al., 2020). As cultivated under high night temperatures, wheat plants lose 20% of their grain weight as compared to normal temperatures, while, decreasing trend in seed setting of wheat was observed in high temperature conditions during anthesis in wheat (Sun et al*.,* 2018). The reduction in grain yield up to 39%, fifty percent reduction in number of grains per spike, twenty four percent reduction in harvest index was observed in one report by Pradhan et al. *(*2015). A typical trend of reduction in number of days to booting, flowering, maturity and harvesting is main effect of heat on wheat. Due to late sown conditions grain filling duration window in wheat gets significantly decreased and affects yield greatly.

Wheat plants often face heat and drought stress simultaneously, especially in regions with arid or semi-arid climates. The combined effect can be more detrimental than either stress alone, as both impact water-use efficiency, photosynthesis, and grain development. Breeding and management practices focus on developing wheat varieties with combined heat and drought tolerance for sustainable productivity. Table 1 summarizes the key differences between heat stress and drought stress.

Germplasm screening for heat tolerance

Evaluation of indigenous and foreign germplasm for heat tolerance is crucial since genetic heterogeneity for heat tolerance may exist within wheat genotypes.

Various screening methods at seedling stage are found effective while selecting germplasm for heat tolerance viz. carbon discrimination method, screening by dry weight, screening through canopy temperature depression method, screening by observing chlorophyll content of leaf, chlorophyll fluorescence of wheat etc.

Leaf senescence, CTD, CT, MTS, grain filling duration are some important screening methodologies for tolerant germplasm in wheat at later stages (Driedonks et al., 2016; Narayanan 2018).

Relation between physiological parameters and heat stress

1- SPAD:

The chlorophyll meter, commonly referred to as a SPAD meter, is a compact and portable tool designed for measuring leaf greenness, which corresponds to the relative chlorophyll concentration in leaves. Unlike traditional destructive methods, this diagnostic tool offers significant savings in terms of time, space, and resources.

The SPAD meter operates by measuring the light transmittance through leaves at two distinct wavelengths: 650 nm and 940 nm. These wavelengths are selectively absorbed by chlorophyll, allowing the device to estimate the chlorophyll content in the leaf. Additionally, the SPAD meter provides insights into leaf nitrogen content, as chlorophyll concentration is closely related to the nitrogen status of plants. This nondestructive approach has become a valuable resource in agricultural and environmental studies (Netto et al., 2005).

2- Canopy temperature:

Canopy and organs temperature (flag leaf, peduncle and spike) can be recorded instantaneously with a hand-held infrared thermometer. A study was conducted which showed high CTD (Canopy Temperature Depression) values in Stay Green genotypes under heat stress conditions which concluded that Stay Green is highly associated with CTD (Dolferus et al., 2011). A positive correlation of canopy temperature depression was found with stomatal conductance and grain yield (Bonari et al., 2020).

3- NDVI:

It is a type of optical sensor unit. It is measured generally in two stages. Firstly, after one month of sowing and secondly, one fortnight after anthesis. Figure 2 shows NDVI values at different stages in wheat crop (Aranguren et al. 2020).

4- Heat susceptibility index (HSI):

HSI of individual genotypes can be calculated by the method suggested by Fischer and Maurer (1978). The genotypes that have high positive HSI values are susceptible to higher temperature and vice versa. If HSI value is < 0.5, then the genotype is highly stress tolerant, if HSI $> 0.5 < 1.0$, it is moderately stress tolerant, and if HSI > 1.0, it is susceptible to heat stress.

5- Heat response index (HRI):

It is a formula/index based on the genotypic response to heat. This formula was first used by Bidinger et al. (1987). Based on genotypic response the germplasm under screening is categorized under groups comprising of genotypes which escape heat, genotypes which resist heat and genotypes having mechanism of tolerance to heat (Munjal and Dhanda, 2016).

6- Stress tolerance (TOL):

TOL was computed using the formula given by Hossain et al. (1990). The genotypes having high values of TOL show higher yield reduction.

According to study conducted by Shehrawat et al. (2020), for a heat tolerant genotype, heat susceptibility index and stress tolerance parameters should be on the lower side, as these parameters are negatively correlated with grain yield. While, the parameters like heat response index, heat tolerance index etc. are positively correlated with grain yield. Therefore, the values of HTI, HRI should be on higher side.

Breeding methods adopted in heat stress

Basically, three types of strategy are adapted by plants to combat heat stress

1- Escape mechanism: Plants undergo physiological, morphological, biochemical and biological modifications in their genotypes and escape heat stress duration. Plant completes its life cycle before detrimental effects of heat and escape.

2- Defense mechanism: Various heat shock proteins, reactive oxygen species gets activated and increase in their levels in plant to combat heat stress. Plants produce ROS in response to heat stress. Also, the heat shock proteins respond rapidly to heat stress.

3- Tolerance: It refers to morphological, biological, phenological, biochemical as well as physiological modifications in plant to tolerate detrimental effects of heat and to maintain cell turgor so as to maintain its production levels (Soni et al., 2023)

To prevent denaturation of proteins due to heat stress, protein folding is favoured through chaperones. Plant start producing more heat shock proteins and activity based on HSP's gets enhanced. All the above-mentioned activities are significantly enhanced with seed priming in nutrient rich media (Chakraborty and Dwivedi 2021). The mechanism of photosystem II is prevented from damage due to special types of heat shock protein i.e sHSP's. It prevents protein damage and ensure high photosynthetic rate of the plants by regularizing electron transport chain. It also ensures proper ATP synthesis and plants grow normally (Haslbeck and Vierling, 2015).

Morphological adaptations

- good seed potential
- proper vegetative growth
- leaf rolling
- inhibited early leaf senescence
- better biomass accumulation

Physiological alteration

- better tillering habit
- increase membrane thermostability
- better photo assimilate translocation
- active photosynthetic metabolism

Biochemical alteration

- sustaining high chlorophyll content
- enhanced activity of soluble starch synthase enzyme
- ROS scavenging and detoxication

Molecular alteration

- activation of stress responsive proteins
- protein folding and regeneration, denaturation of abnormal protein
- inhibition of apoptosis
- protection of cytoskeleton

Conventional breeding:

Breeding programmes are typically carried out in an area that is comparable to the crop's growing region. Accordingly, breeding lines should be chosen for heat tolerance while the weather is hot (Mickelbart et al., 2015).

To select superior genetic stock against heat stress, stable performance of plant in terms of yield in heat stress conditions is a conventional approach to focus upon (Mishra et al., 2014). Masthigowda et al. (2022) proposed that pollen viability is a crucial characteristic for screening wheat genotypes' tolerance to withstand heat stress. According to another study conducted by Ul Hassan et al. (2021), high potential grain weight under heat stress may potentially be a more important criterion in selecting cultivars for heat tolerance and resilience to changing future climate conditions. It is necessary to identify donor genotypes for heat tolerance through genetic resource screening. Establishing heat stress tolerant genotypes by examining regional genotypes of wheat that are highly adapted to heat stress is the first stage in developing a wheat breeding programme for heat stress (Bita and Gerats 2013).

Advanced breeding:

To create heat-stress-tolerant cultivars, advanced breeding techniques includes GWAS and marker-assisted backcrossing. Genome diversity among species yielded in genes/QTL's responsible for heat tolerance in wheat (Wahid et al., 2007). SSR and AFLP markers were used in various studies to map these QTL's (Lu et al*.,* 2020). Advance markers such as, DArT (Diversity Arrays Technology markers), SNP's (Single Nucleotide Polymorphism), NGS (Next Generation Sequencing), etc. are found promising in breeding heat tolerant genotypes in recent years in wheat crop (Cabral et al*.,* 2018; Sonah et al., 2012). Genomic selection may be coupled with GWAS or QTL studies to better incorporate trait of heat tolerance in novel genotypes. These methods can be found effective for pyramiding genes from diverse genome size (Bassi et al*.,* 2016).

With the complexity of the underlying heat tolerance mechanisms, genome wide analysis has proven to be a valuable method for identifying heat stress responsive genes (Wang et et al., 2015). Research is also oriented towards functional analysis of genes for heat tolerance in background of transgenics (Clavijo et al*.,* 2017). Study of overexpression of gene related to heat tolerance and genes contributing sense and response to heat are also revolutionary and trending areas of research now a days (Zang et al., 2017).

Deep insights to understand mechanism of heat tolerance at transcriptomic, metabolomic and genomic levels is need of the hour. It will better respond to ongoing efforts to combat heat (Bhardwaj et al., 2021). All chemical strategies linked to heat stress tolerance in wheat plants start at a few heat stress tolerance genes that contain genomic DNA (Deshmukh et al., 2014). Genes contributing heat tolerance in wheat has been determined through studies of genome expression and genomic screen (Yeh et al*.,* 2012). Heat tolerance genes' mRNAs (transcript products) are translated into functional proteins, which in turn produce proteomes (proteomics), which are responsible for the tolerance to heat stress. Plants use small non-protein coding RNAs, or microRNAs, to show some post transcriptional gene expression. Understanding the mechanisms underlying wheat's heat tolerance is improved by research on microRNAs and micromics (Chinnusamy et al*.,* 2007). According to Abdulrahman et al. (2020), metabolomics is an additional omics technique that can be applied to the phenotyping the traits contributing to heat tolerance in genetically modified plants. To elucidate the response pattern of plants against abiotic as well as biotic stress and to determine the function of genes contributing to trait of concern, metabolomics is the better possible way out.

Traditional breeding procedures, which might take more than ten years to generate high- performing cultivars with targeted features, are proving to be ineffective and become a barrier in developing heat-tolerant wheat varieties. However, a new breeding method known as 'speed breeding' has been developed to shorten the generation time, accelerate the development, marketing, and commercialization of improved plant varieties (Imam et al., 2024). It manipulates temperature, light duration, and intensity to accelerate the crop development. Every year, this speed breeding method can produce up to six generations of bread wheat (*Triticum aestivum*) and durum wheat (*Triticum durum*) (Watson et al., 2018). Recently, genome editing tools and resources such as CRISPR-Cas9, TILLING, and others have been used to improve wheat heat tolerance (Liang et al*.,* 2017). As a result, the combination of these advanced tools and speed breeding may provide scientists with an effective inducement to conduct heat tolerance research in wheat.

Transgenic Approach:

In comparison to traditional breeding and marker-assisted selection programmes, genetic engineering's direct introduction of a limited number of genes looks to be a more desirable and quick way to improve stress tolerance. Current engineering procedures rely on the transfer of one or more genes encoding biochemical pathways or signaling pathway endpoints that are regulated by a constitutively active promoter. These gene products offer protection against environmental challenges, either directly or indirectly. Transgenic technology has developed as an effective technique for enhancing crop genetics in order to enhance survival, growth, and yield (Sun et al., 2022). However, little progress has been made towards developing heat-tolerant transgenic wheat plants.

Conclusions

Breeding for heat stress in field crops is a major challenge at global level. The heat stress effect are usually confounded with water stress. Heat stress impairers photosynthesis, carbohydrates, proteins, lipid metabolism and cell membrane functions that lead to decline in plant growth and consequently grain yield. To maintain high yields with better response to heat stress in crops is best possible through various metabolic, metabolomic, transcriptomic, biochemical and molecular responsive mechanisms. In order to infuse tolerance against heat stress in wheat genotype, assembly of gene constellations determining heat shock responses, membrane thermal stability and vernalization responses should be accommodated in agronomic elite wheat genotypes. Different agronomic options, as well as biochemical and molecular approaches, must be combined to investigate the realistic response of plants against heat stress at the field level. Collaborative team efforts from plant breeders, biotechnologists, molecular biologists and physiologists would aid in the developing novel thermo-tolerant genotypes in wheat to combat heat stress globally.

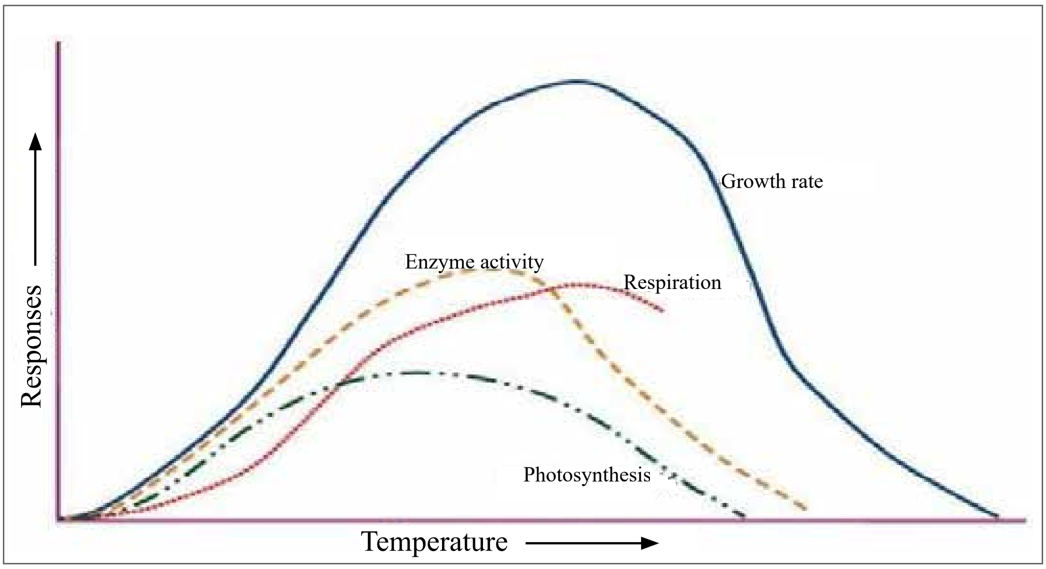

Figure 1. Effect of temperature on various physiological processes and growth rate of plants (Fitter and Hay, 2012).

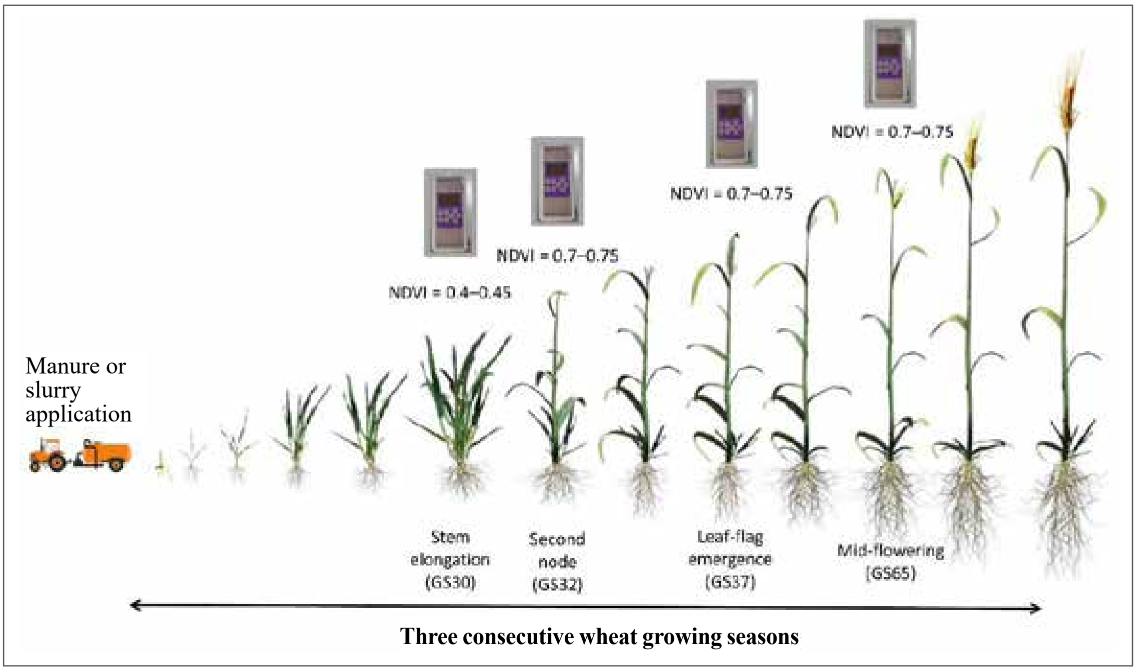

Figure 2. NDVI values at different stages in wheat crop (Aranguren et al., 2020).

Table 1. The key differences between heat stress and drought stress.

Aspect	Heat Stress	Drought Stress
Primary Cause	High temperatures	Low water availability
Impact on Physiology	Disruption of enzymatic and metabolic processes	Disruption of water uptake and retention
Key Mechanism	Production of heat shock proteins and antioxidant activity	Root architecture and osmotic adjustment
Critical Stage	Flowering and grain filling	Any growth stage, but often during flowering or grain filling
Visible Symptoms	Leaf scorching, reduced grain size	Leaf wilting, rolling, yellowing

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