



Aftermath of terminal heat stress on Indian mustard (*Brassica juncea* L.) : A brief review

Narender Mohan, Nisha Kumari*, Minakshi Jattan, Ram Avtar and Vineeta Rathore

CCS Haryana Agricultural University, Hisar 125 004, India

*Corresponding author: nishaahlawat211@gmail.com

(Received: 19 June 2019; Revised: 07 October 2019; Accepted: 25 November 2019)

Abstract

Abiotic stresses are often interrelated, either individually or in combination, they cause morphological, physiological, biochemical and molecular changes that adversely affect plant growth, productivity and ultimately seed yield. Heat, drought, cold and salinity are the major abiotic stresses that induce severe cellular damage in plant species, including crop plants. High temperature especially terminal heat stress is the second most important stress next to drought. It has negative effect on plant growth due to the harmful effect on plant development. It is a critical factor for plant productivity also. Generally plants respond to heat stress through developmental, biochemical and physiological changes and the type of response depends on several factors such as stress intensity, stress duration and genotype. It poses serious threats to the sustainability of crop production. The increasing threat of climate change is already having a substantial impact on agricultural production worldwide, waves cause significant yield losses with great risks for future global food security. In this review, detrimental effects of terminal heat stress on Indian mustard are discussed in terms of morpho-physiological, yield and biochemical attributes.

Key words: Abiotic stress, crop production, crop yield, mustard and terminal heat stress

Introduction

Plants are constantly exposed to various biotic and abiotic stresses. The abiotic stresses viz. drought, salinity, temperature fluctuations, heavy metals and nutrient deficiencies etc. are the main reasons for yield losses in crop plants. Of the major forms of abiotic stress plants are exposed to in nature, heat stress has an independent mode of action on the physiology and metabolism of plant cells. Although frequently, heat stress is compounded by additional abiotic stresses such as drought and salt stress, it is important to unravel the independent action and biological consequences of high temperature in order to ameliorate the effects of combined abiotic stress. The susceptibility to high temperatures in plants varies with the stage of plant development, heat stress affecting to a certain extent all vegetative and reproductive stages. The observed effects depend on species and genotype, with abundant inter and intra-specific variations (Sakata and Higashitani, 2008). These stresses have a long term impact on plants development and advancement regardless of whether plant is presented to them for a negligible span (Wang *et al.*, 2003). These stresses modify plant metabolism prompting negative impact on development, advancement and finally efficiency of plants. Plants have adopted various morphological, physiological and biochemical

adjustments to handle these stresses and hence making plant survivability feasible (Huber and Bauerle, 2016). Morphological and physiological adjustments are mainly performed through avoidance mechanism that provides an escape to stresses like water and heat. The increased root system, reduced stomata number and conductance, decreased leaf area, increased leaf thickness, and leaf rolling or folding to lessen evapotranspiration (Goufo *et al.*, 2017). The cuticular wax biosynthesis, on the surfaces of the aerial plant parts, is also strictly associated with an adaptive response (Lee and Suh, 2013). Tolerance traits maintain tissue hydrostatic pressure, by cellular and biochemical modifications, mainly through osmotic adjustments (Blum, 2017). Worldwide environmental change especially high temperature is anticipated to increment by around 1-30° C by the mid twenty-first century and by 2-50° C by the late twenty-first century.

Out of various abiotic stresses, high temperature is the second most vital stress by next to drought influencing plant productivity around the world. Consequently, it presents genuine dangers to the supportability of yield creation more than some other factors in agriculture (Bhatnagar and Mathur, 2008; Ahmad and Prasad, 2012). Brassica grows under diverse agro-environmental circumstances, for example, timely sown/late sown, rainfed/irrigated, sole and mixed crop with cereals i.e.

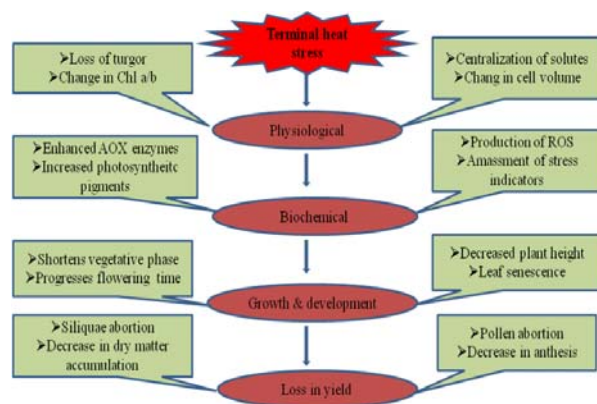


Fig.1. The detrimental effects of terminal heat stress on crop plants

wheat, barley etc. and *Rabi* (October-April) pulses (Chickpea, Lentil etc.). High temperature is the primary imperative at germination as well as at grain filling stage due to vulnerability during pollen production, grain development, anthesis and fertilization leading decrease in crop yield. Terminal heat stress induce overproduction of reactive oxygen species (ROS), which are extremely reactive and toxic, causing damage to proteins, lipids, carbohydrates and DNA and ultimately resulting in oxidative stress (Zlatev and Lidon, 2012). Oxidative stress has negative impact on plant development, survival and consequently crop productivity. Oxidative stress is commonly counteracted by two different processes, prevention or avoidance of ROS formation, including detoxifying/scavenging enzymes and several antioxidants to handle the toxic effect of ROS (Mittler, 2002). Every degree ascend in normal temperature in a developing season, may lessen the crop yield upto 17 %. This distinction in yield is ascribed to a great extent to the negative natural conditions, which make conceivably harming physiological changes inside plants (Lobell and Asner, 2003). The different morphological, physiological, biochemical and yield attributes get affected by high temperature stress at the terminal stage. The adverse effects of terminal heat stress are depicted in Fig.1

Morpho-physiological attributes

Plant water status is one of the real factors under changing temperature (Mazorra *et al.*, 2002). Heat stress induces changes in respiration and photosynthesis and thus leads to a shortened life cycle and diminished plant productivity (Barnabas *et al.*, 2008). The cell water deficiency results in the centralization of solutes, change in cell volume, change in membrane integrity, loss of turgor and interruption of water potential gradients (Raymond and Smirnov, 2002). The increased temperature under late

sown condition of crop results in critical abatement in the relative water content in leaves of Indian mustard (Sairam *et al.*, 2000). Alteration in leaf water potential shows the negative effect of temperature stress on root hydraulic conductance even under optimal condition of the water supply from soil and relative humidity conditions (Wahid and Close, 2007). There is a critical difference in relative water content of *B. juncea* that ranged from 52.28 % (RGN-330) to 118.61 % (Pro-5222) under states of high temperature at terminal stage (Kavita and Pandey, 2017). Higher relative water content observed in leaves of Indian mustard is a decent marker of heat resistance (Ram *et al.*, 2012; Kumar *et al.*, 2013).

Development and advancement of plant rely on cell enlargement, cell division and these processes are sensitive to water deficiency condition. Leaf water potential was impacted by water status of the soil (Sharma and Pannu, 2007). Loss of water is a lot quicker amid the day than around evening time because of this there is improved transpiration rate, diminishing water capability of the plant. Timely sowing is the best time to study temperature stress, because too early sowing and too late sowing of crop leads to reduction in vegetative stage, grain filling stage and reduced osmotic potential (Tobias and Niinemets, 2005). Photosynthetic pigments are essential to plants, fundamentally to harvest light and produce reducing powers. Any constraint in chlorophyll content (chlorophyll 'a' and 'b') can limit photosynthesis that will additionally constrain plant growth during heat stress. Photochemical responses in thylakoid lamellae and carbon metabolism in stroma of chloroplast are considered as the essential site of damage during high temperature (Wise, 1995). The distinctions in the photosynthetic pattern under heat stress have appeared to be related with the loss of chlorophyll and change in chlorophyll a/b proportion because of untimely leaf senescence (Harding *et al.*, 1990). The temperature stress fundamentally decreased the chlorophyll content in mustard (Kumar, 2010).

There is variability in photosynthetic rate in wheat cultivars when exposed to high temperature as observed by Wardlaw *et al.* (1980). Chlorophyll content in Indian mustard ranged from 4.83 to 9.06 mg/gFW under terminal heat stress (Kavita and Pandey, 2017). The high chlorophyll content is ideal for stress conditions (Kumar and Srivastava, 2003). Terminal heat stress influencing different physiological traits additionally have articulated effect on the oil content at seedling stage. In Indian mustard, the oil content was higher in tolerant genotypes when compared with sensitive genotype under heat stress. The late sowing condition likewise diminished the

oil content in Australian cultivars of oil seed rape (*B. napus*) (Mendham and Salisbury, 1981). Decline in oil content of Brassica has been observed under high temperature stress at grain filling stage (Heenam and Armstrong, 1993). Mohan (2017) observed that tolerant genotypes *i.e.* RGN-368 and RH-1566 showed less percent decrease, in comparison to the sensitive genotypes.

Yield attributes

Seed yield is a quantitative attribute, which is highly impacted by the genotype, ecological effect and by environmental interaction. Number of siliqua/plant is a fundamental segment in deciding seed yield of rapeseed mustard. Higher number of primary and secondary branches/plant under timely sowing condition in Indian mustard is likewise a noteworthy character for higher yield (Kumar *et al.*, 2004). Kumari *et al.*, (2012) directed a field investigation to assess the impact of various sowing dates on cultivars of *B. juncea* and detailed that the most noteworthy plant height (209 cm) under timely sowing condition *i.e.* 10th October and least plant height was seen (186 cm) under late sowing condition (30th October). The plant height was negatively affected by sowing time in Canola (Abdul *et al.*, 2013). The high temperature at the season of harvest resulted in plant height decrease by 22.8 % (Singh *et al.*, 2014). There is a negative correlation of sowing time and plant height under late sowing condition in Indian mustard (Alam *et al.*, 2015). Seed yield is significantly decreased in *B. juncea* under stress with maximum reduction observed in RH-0749 (20.11 %) and RH-1134 (21.37 %) whereas; minimum reduction was seen in RH-1566 (7.72 %), and RGN-368 (8.27 %) (Mohan, 2017).

A significant reduction of 13 % and 50 % was observed in seed yield of Indian mustard sown on two different dates 1st November and 15th November, respectively (Kumar *et al.*, 2013). They additionally presumed that the tolerant genotypes gave higher seed yield than sensitive genotypes. In Indian mustard the thermo-tolerance ability has been checked by studying different parameters including seed yield under heat stress (Ram *et al.*, 2014). There is a significant decrease in seed yield and other yield characteristics under late sown condition (26 November) when compared with timely sown condition (26 October) and this decline is due to high temperature stress prevailing at late sown conditions (Singh *et al.*, 2014). There is a significant decline in productivity of Indian mustard including almost all yield attributes under late sown condition when compared to timely sown condition (Lallu and Dixit, 2008). There is a noteworthy negative impact of temperature stress because of late sown on seed yield in Indian mustard (Gawariya *et al.*, 2015; Khayat *et al.*, 2015).

Even the Phenological studies including days to 50 % flowering and maturity describes effect of high temperature stress on crop yield. Mustard vegetation cycle has been classified into three distinctive development stages, sowing to seedling emergence; seedling emergence to flowering and flowering to maturity (Kumar, 2016). Flowering is the most sensitive stage for temperature stress bringing about pollen abortion; decrease in anthesis and fertilization that further has a declining impact on crop yield. High temperature in Brassica caused flower abortion with apparent loss in seed yield (Rao *et al.*, 1995). Delay in sowing time shortens vegetative phase, progresses flowering time and decrease in dry matter accumulation and regularly caused siliquae abortion, bringing about lower yield (Babu, 1985). A study on effect of variable sowing dates (7, 14 and 21 October) in case of mustard cultivars revealed that the crop sown on 14th and 21st October delayed days to 50 % flowering as compared to sowing on 7th October (Kumar *et al.*, 2004). Mohan (2017) contemplated different yield attributes *viz.* fundamental shoot length, primary and secondary branches, number of siliqua/main shoot, seeds/siliqua, siliqua length, thousand seed weight and seed yield/plant which demonstrated a significant reduction under late sown condition.

Biochemical attributes

Biochemical compounds which impart defense against reactive oxygen species developed under terminal heat stress have been categorized into enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants includes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR) and non-enzymatic antioxidants includes carotenoids, ascorbic acid and proline etc. Different investigations have proven the role of these antioxidants under stress conditions.

Carotenoids are class of isoprenoid molecule which is synthesized by photosynthetic and non photosynthetic life forms (Andrew *et al.*, 2008). Carotenoids act both as accessory light harvesting pigments as well as antioxidants (Pandhir and Shekhon, 2006). Plants grown under irradiation showed high carotenoid content (Adams and Demmig-Adams, 1992). High carotenoid content was reported in those plants which were subjected to abiotic stress like drought in wheat (Anu, 2000). Carotene helps in the protection in photosynthetic tissue by direct quenching of triplet chlorophyll, which prevents the formation of singlet oxygen and hence prevent oxidative damage. Mohan (2017) reported a significant increase in ascorbic acid, proline and carotenoid content in all the

genotypes with a higher increase seen in thermo-tolerant genotypes as compared to thermo-sensitive genotypes.

Ascorbic acid synthesized in cytosol is a noteworthy constituent of plant cell which is real constituent of plant cell which is translocated to the apoplast later (Takahama, 1996). Biological role of ascorbic acid is to act as a reducing agent, donating electrons to various enzymatic and non-enzymatic reactions. Presence of glutathione in cells keeps up ascorbate in a reduced form. Experiment on heat acclimated versus non acclimated cool season turf grass species revealed that the former had lower generation of ROS because of increased synthesis of ascorbate and glutathione (Xu *et al.*, 2006). Decline in ascorbic acid content was observed as the temperature increased in stressed wheat genotypes (Sairam *et al.*, 2000) and in soyabean seeds (Yadav *et al.*, 2006). The ascorbic acid content increased significantly in *Brassica juncea* developed under high temperature stress but the increase was found higher in tolerant genotypes i.e. (29.31 %) in BPR-542-6 when contrasted with sensitive genotype RGN-152 (15.38 %) (Rani *et al.*, 2016).

Proline is considered as one of the most remarkable metabolite, which tends to increase under various abiotic stresses. Accumulation of this low molecular weight compound is an adaptive mechanism against stress (Rasheed *et al.*, 2010). Terminal heat stress prompts a few changes in plants. So to increase plant tolerance to abiotic stress and to maintain a high relative water content and osmotic potential, plants may accumulate proline (Zlatev and Lidon, 2012). Accumulation of proline is mainly reported during environmental stress like heat (Wahid and Close, 2007). A correlation has been seen between plant stress tolerance and the proline accumulation by Tyagi *et al.* (1999) in Brassica, Kaushal *et al.* (2011) in chickpea and Ahmed and Hasan (2011) in wheat.

Hydrogen peroxide (H_2O_2) is produced by the reduction of superoxide radical by SOD and as a product of photorespiration; it is normally reactive having a long half life. It acts as signaling molecule under low concentration and leads to programmed cell death when the concentration is high. Highly reactive oxygen species capable to cause oxidative damage involves superoxide, per hydroxyl radical, hydrogen peroxide, hydroxyl radical, peroxy radical and singlet oxygen. Hydrogen peroxide content may increase during abiotic stresses like cold in cucumber (Lee and Lee, 2000), excess light exposure in pea (Hernandez *et al.*, 2004) and heat stress in wheat (Li *et al.*, 2004). Large amount of H_2O_2 was seen under stressed condition such as heat stress reported by Kumar (2010) in Indian mustard and also increase in H_2O_2 was

seen more in sensitive genotypes as compared to tolerant genotypes of *B. juncea* (Rani *et al.*, 2016). The more increase in H_2O_2 was observed in thermo-sensitive genotypes i.e. RH-1134 (77.2 %) and RH-0749 (67.9 %) as compared to the thermo-tolerant genotypes i.e. RGN-368 (44.3 %) and RH-1566 (56.5 %) (Mohan, 2017).

Electrolyte leakage is a hallmark of stress response in intact plant cells. It is the amount of ion leakage from plant cells, determining the cell membrane stability (Zhang *et al.*, 2006). Electrolyte leakage is mainly related to K^+ efflux from plant cells, which is mediated by plasma membrane cation conductance. Low cell membrane integrity is caused by ROS generated during stress (Liu and Huang, 2000). Decrease in cell membrane integrity under high temperature in cowpea is because of degradation of photosynthetic apparatus associated with the production of free radicals (ROS) (Camejo *et al.*, 2006). There is a negative correlation between test weight (1000 seed weight) and electrolyte leakage under terminal heat stress tolerance in Indian mustard (*B. juncea*) (Kavita and Pandey, 2017). Increase in membrane damage due to increasing stress leads low seed yield (Sharma and Sardana, 2012). Malondialdehyde is the product of peroxidation of unsaturated fatty acids in phospholipid and is responsible for cell membrane damage therefore, utilized as a suitable biomarker for lipid peroxidation (Kumar, 2010). The ROS generated during high temperature stress reacts with phospholipid bilayer due to presence of unsaturated lipids in membranes and cause lipid peroxidation leading to accumulation of MDA (Liu and Huang, 2000). It has been reported in *B. juncea* that under high temperature in tolerant genotypes showed low accumulation of MDA and thus registers lesser oxidative damage is found higher in sensitive genotypes (Wilson *et al.*, 2012).

Reactive oxygen species plays not only damaging role but also key signaling roles in plants and their cellular concentration is controlled by a complex network of ROS metabolizing enzymes found in several different cellular compartments. Generation of ROS has been observed in electron transport system of chloroplast and mitochondria (Kumar, 2010). Plants have developed both enzymatic and non-enzymatic mechanisms to scavenge the rapidly evolving ROS. These enzymes, includes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), and glutathione reductase (GR) (Zhang *et al.*, 2006).

Superoxide dismutase is a metalloenzyme. It is the most effective intercellular enzymatic antioxidant which is ubiquitous in all aerobic organisms and in all subcellular

compartments prone to ROS mediated oxidative stress. It provides the first line of defense against the toxic effects of elevated levels of ROS (Van Camp *et al.*, 1996). In plants there are three major categories of SOD located in different cell compartments, Fe-SODs in chloroplast, Mn-SODs in mitochondria and Cu/Zn-SOD isoforms are primarily localized in cytosol and chloroplast. SOD, a major scavenger of superoxide radical ($O_2^{\cdot-}$), catalyzes the conversion of $O_2^{\cdot-}$ to H_2O_2 and O_2 . Activity of SOD is temperature sensitive and reported to increase significantly under terminal heat stress. There is a significant increase in SOD activity under high temperature and the increase was found maximum in the tolerant varieties of Indian mustard (Sairam *et al.*, 2000). Similar observations reported by Goyal and Asthir, (2010) and Ahmad and Prasad (2012) in wheat, that SOD activity was more enhanced in the cultivar that has better tolerance to high temperature stress in wheat plants. It has been reported that the SOD activity increased under high temperature stress but the increase was significantly higher in tolerant genotype of Indian mustard (Rani *et al.*, 2016; Mohan, 2017).

Peroxidases are another group of non-chloroplastic enzymes that detoxify H_2O_2 in the cytosolic part of the cell. They are non-specific in utilizing electron donor for oxidation of H_2O_2 . Increase in peroxidase activity was reported (Chaitanya *et al.*, 2001) in mulberry and (Mazorra *et al.*, 2002) in tomato cultivars under high temperature stress. Increase in peroxidase activity upto 52.3 % in tolerant genotypes and 21.1 % in sensitive genotypes was reported under heat stress in *B. juncea* (Wilson *et al.*, 2012).

Catalase is also a non chloroplastic enzyme present largely in plant tissue except chloroplast. Catalase is tetrameric heme containing enzyme with the potential to directly dismutate H_2O_2 into H_2O and O_2 (Garg and Manchanda, 2009) and is indispensable enzyme for ROS detoxification during stressed conditions. It is present in three different isoforms (CAT1, CAT2 and CAT3) in which CAT1 and CAT2 are found in peroxisomes (involved in Beta-oxidation of fatty acids, photorespiration and purine catabolism), whereas CAT3 is found in mitochondria. Catalase has the highest turnover rate of about 6 million molecules of H_2O_2 converted to H_2O and O_2 per minute. The catalase activity has been significantly higher in tolerant genotypes of mulberry cultivars under high temperature stress (Chaitanya *et al.*, 2001). The increase in catalase activity was observed under terminal heat stress with maximum increase in tolerant genotypes (Kumar, 2010; Mohan, 2017). Increase in catalase activity

under heat stress in Brassica was also reported by Rani *et al.* (2016) and concluded that increase was more (41.3 %) in tolerant than sensitive (17.6 %) genotypes.

Ascorbate peroxidase is one of the specific enzymes that scavenge chloroplastic H_2O_2 . It specifically uses ascorbate as a physiological reductant and is considered as a crucial component in the metabolic defense against oxidative stress. It acts by a series of coupled redox reactions, both in photosynthetic and non-photosynthetic tissues. Ascorbate peroxidase activity in *B. juncea* under stress conditions showed a remarkable increase (Mobin and Khan, 2007). Exposure of crop plants to high temperature stress resulted in increase in APX activity in mustard seedlings (Dat *et al.*, 1998). Rani *et al.*, 2016 studied *B. juncea*, at seedling stage, and observed a significant increase in APX activity in tolerant genotypes of *B. juncea*. Kumar (2010) while studying *B. juncea* under different sowing dates also reported a high increase of APX activity in tolerant genotypes.

Glutathione reductase is a flavo-protein oxidoreductase. Glutathione reductase assumes a vital job in the age of GSH and consequently secures against oxidative worry by keeping up the ASH pool. Glutathione reductase is restricted overwhelmingly in chloroplast, yet little measure of this protein has likewise been found in mitochondria and cytosol. Glutathione reductase (GR) assumes an essential job in deciding the resilience of a plant under different burdens (Chalapathi-Rao and Reddy, 2008). Enhanced GR activity has been observed in tolerant genotypes of *B. juncea* on exposing to terminal heat stress (Mohan, 2017).

Conclusion and future perspectives

The different abiotic stresses especially terminal heat stress significantly affects the morpho-physiological processes of some important Brassica species. Development and identification of abiotic stress tolerant cultivars are important economic goals for our globe. The morphological and agronomical study of *Brassica* sp. performing under environmental extremes could lead the research and development of new stress-tolerant cultivars. With the advent of new technologies such as genomics and genetic transformation, significant progress has been made in development of improved *Brassica* sp. against wide range of abiotic stresses.

References

- Abdul S, Cheema MA, Wahid MA, Saleem MF, Ghaffari MA, Hussain S and Arshad MS. 2013. Effect of sowing time on seed yield and oil content of canola varieties. *J Glob Innov Agric Soc Sci* **1**: 1-4.

- Adams WW and Demmig-Adams B. 1992. Operation of the xanthophyll cycle in higher plants in response to diurnal changes in incident sunlight. *Planta* **186**: 390-398.
- Ahmad P and Prasad MNV. 2012. *Abiotic Stress Responses in Plants: Metabolism, Productivity and Sustainability*. Springer Science+Business Media LLC.
- Ahmed JU and Hasan MA. 2011. Evaluation of seedling proline content of wheat genotypes in relation to heat tolerance. *Bangladesh J Bot* **40**: 17-22.
- Alam MJ, Ahmed KS, Mollah MRA, Tareq MZ and Alam J. 2015. Effect of planting dates on the yield of mustard seed. *Int J Appl Sci Biotec* **3**: 651-654.
- Andrew JS, Moreau H, Kuntz M, Pangy G, Lin C, Tanksley S and Mc Carty J. 2008. An investigation of carotenoid biosynthesis in *Coffea canephora* and *Coffea Arabica*. *J Plant Physiol* **165**: 1087-1106.
- Anu. 2000. Response of plant antioxidant defense mechanism to water deficit stress in wheat. M.Sc. Thesis. CCSHAU, Hisar, India.
- Babu LC. 1985 Physiological analysis of growth and development with reference to planting date in rapeseed-mustard. Ph.D. Thesis. Indian Agricultural Research Institute, New Delhi, India.
- Barnabas B, Jager K and Feher A. 2008. The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell Environ* **31**: 11-38.
- Bhatnagar P and Mathur VV. 2008. Transgenic approaches for abiotic stress tolerance in plant: reaspect and prospects. *Plant Cell Rep* **27**: 411-424.
- Blum A. 2017. Osmotic adjustment is a prime drought stress adaptive engine in support of plant production: osmotic adjustment and plant production. *Plant Cell Environ* **40**: 4-10.
- Camejo D, Jimenez, A, Alarcon JJ, Torres W, Gomez JM and Sevilla F. 2006. Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. *Funct Plant Biol* **33**: 177-187.
- Chaitanya KV, Sundar D, Masilamani S and Reddy RA. 2001. Variation in heat stress induced antioxidant enzyme activities among three mulberry cultivars. *Plant Growth Regul* **36**: 175-180.
- Chalapathi-Rao ASV and Reddy AR. 2008. Glutathione reductase: A putative redox regulatory system in plant cells. pp. 111-147. In: "*Sulfur Assimilation and Abiotic Stress in Plants*". Springer-Verlag. Berlin pp: 372.
- Dat JF, Lopez-Delgado H, Foyer CH and Scott IM. 1998. Changes in salicylic acid and antioxidants during induced thermotolerance in mustard seedlings. *J Plant Physiol* **118**: 1455-1461.
- Garg N and Manchanda G. 2009. Reactive oxygen species generation in plants: Boon or bane? *Plant Biosys* **143**: 81-96.
- Gawariya SC, Chopra NK, Chopra N and Harika AS. 2015 Effect of date of sowing and crop geometry on growth and yield parameters of forage mustard (Var. *Chinese Cabbage*). *African J Agri Res* **10**: 3292-3295.
- Goufo P, Moutinho-Pereira JM, Jorge TF, Correia CM, Oliveira MR and Rosa EAS. 2017. Cowpea (*Vigna unguiculata* L. Walp.) metabolomics: osmoprotection as a physiological strategy for drought stress resistance and improved yield. *Front Plant Sci* **8**:586.
- Goyal M and Asthir B. 2010. Polyamine catabolism influences antioxidative defense mechanism in shoots and roots of five wheat genotypes under high temperature stress. *Plant Growth Regul* **60**: 13-25.
- Harding SA, Guikema JA and Paulsen GM. 1990. Photosynthetic decline from high temperature stress during maturation of wheat and Interaction with senescence process. *Plant Physiol* **92**: 648-653.
- Heenam DP and Armstrong EL. 1993. Sowing time effects on yield and quality of canola and linseed. In: "*9th Australian Research Assembly on Brassicas*". (Wratten N & Mailer RJ eds) Wagga Wagga, New South Wales, pp: 83-86.
- Hernandez JA, Escobar C, Creissen G and Mullineaux PM. 2004. Role of hydrogen peroxide and the redox state of ascorbate in the induction of antioxidant enzymes in pea leaves under excess light stress. *Funct Plant Biol* **31**: 359-368.
- Huber AE and Bauerle TL. 2016. Long-distance plant signaling pathways in response multiple stressors: the gap in knowledge. *J Exp Bot* **67**: 2063-2079.
- Kaushal N, Gupta K, Bhandari K, Kumar S and Thakur P. 2011. Proline induces heat tolerance in chickpea (*Cicer arietinum* L.) plants by protecting vital enzymes of carbon and antioxidative metabolism. *Physiol Mol Bio Plant* **17**: 203-213.
- Kavita and Pandey A. 2017. Physiological attributes for screening of Indian mustard [*B. juncea* (L) Czern & Coss.] genotypes during terminal heat stress. *Intl J Curr Micro Appl Sci* **6**: 2908-2913.
- Khayat M, Rahnema A, Lorzadeh S and Lack S. 2015. Physiological Indices, Phenological Characteristics and Trait Evaluation of Canola Genotypes Response to Different Planting Dates. The National Academy of Sciences, India.
- Kumar A, Singh B, Yashpal and Yadava JS. 2004 Effect of sowing time and crop geometry on tetralocular Indian mustard (*B. juncea*) under south-west Haryana. *Ind J Agri Sci* **74**: 594-96.

- Kumar Ajeev. 2016. Morpho-physiological responses of Indian mustard (*B. juncea*) genotypes in different sowing dates. M Sc Thesis. CCSHAU, Hisar, India.
- Kumar N and Srivastava S. 2003. Plant ideotype of Indian mustard (*B. juncea*) for late sown conditions. *Int J Gen* **63**: 355.
- Kumar S, Sairam RK and Prabhu KV. 2013. Physiological traits for high temperature stress tolerance in *B. juncea*. *Ind J Plant Physiol* **18**: 89-93.
- Kumar S. 2010. Study of temperature stress tolerance in Indian mustard (*B. juncea*). Ph.D. Thesis. Indian Agricultural Research Institute, New Delhi, India.
- Kumari A, Singh RP and Yashpal. 2012. Productivity, nutrient uptake and economics of mustard hybrid (*B. juncea*) under different planting time and row spacing. *Ind J Agron* **57**: 61-67.
- Lallu and Dixit RK. 2008. High temperature effect at terminal stage in mustard genotypes. *Ind J Plant Physiol* **13**: 151-158.
- Lee DH and Lee CB. 2000. Chilling stress induced changes of antioxidant enzymes in the leaves of cucumber in gel enzyme activity assays. *Plant Sci* **159**: 75-85.
- Lee SB and Suh MC. 2013. Recent advances in cuticular wax biosynthesis and its regulation in *Arabidopsis*. *Mol Plant* **6**: 246-249.
- Li C, Jiao J and Wang G. 2004. The important roles of reactive oxygen species in the relationship between ethylene and polyamines in leaves of spring wheat seedlings under root osmotic stress. *Plant Sci* **166**: 303-315.
- Liu X and Haung B. 2000. Heat stress injury in relation to membrane lipid peroxidation in creeping bentgrass. *Crop Sci* **40**: 503-510.
- Lobell DB and Asner GP. 2003. Climate and management contribution to recent trends in US. *Agri Yield Sci* **299**: 1032.
- Mazorra LM, Nunez M, Hechavarria M, Coll F and Sanchez-Blacon MJ. 2002. Influence of brassinosteroids on antioxidant enzymes activity in tomato under different temperatures. *Biol Plant* **45**: 593-596.
- Mendham NJ and Salisbury PA. 1981. Physiology: Crop development, growth and yield. Pages 11-64 in D. Kimber and DI. McGregor, ed. *Brassica* oilseeds: Production and utilization. CAB International, Slough, UK.
- Mittler R. 2002. Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci* **7**: 405-410.
- Mobin M and Khan NA. 2007. Photosynthetic activity, pigment composition and antioxidative response of two mustard (*B. juncea*) cultivars differing in photosynthetic capacity subjected to cadmium stress. *J Plant Physiol* **164**: 601-610.
- Mohan N. 2017. Biochemical and morpho-physiological changes in Indian mustard [*B. juncea* (L.) Czern & Coss.] under terminal heat stress. M Sc Thesis. CCSHAU, Hisar, India
- Pandhir and Shekhon. 2006. Reactive oxygen species and antioxidants in plants: An overview. *J Plant Biochem Biotech* **15**: 71-78.
- Ram B, Meena HS, Singh VV, Singh BK, Nanjundan J, Kumar A, Singh SP, Bhogal NS and Singh, D. 2014. High temperature stress tolerance in Indian mustard (*B. juncea*) germplasm as evaluated by membrane stability index and excised-leaf water loss techniques. *J Oilseed Brassica* **5**: 149-157.
- Ram B, Singh BK, Singh M, Singh VV and Chauhan JS. 2012. Physiological and molecular characterization of Indian mustard (*B. juncea*) genotypes for high temperature tolerance. *Crop Imp (Special issue) ICASA*: 5-6.
- Rani B, Kumari N, Pooja, Jain V, Dhawan K, Monika, Avtar R, Kumar A and Sheoran P. 2016. Antioxidative system as influenced by high temperature stress in *B. juncea* (L) Czern & Coss. *Trend Biotech Pharm* **10**: 118-125.
- Rao MV, Halle BA and Ormrod DP. 1995. Amelioration of ozone-induced oxidative damage in wheat plants grown under high carbon dioxide. *Plant Physiol* **109**: 421-432.
- Rasheed R, Wahid A, Ashraf M and Basra SMA. 2010. Role of proline and glycinebetaine in improving chilling stress tolerance in sugarcane buds at sprouting. *Int J Agri Biol* **12**: 1-8.
- Raymond MJ and Smirnof N. 2002. Proline metabolism and transport in maize seedlings at low water potential. *Ann Bot* **89**: 813-23.
- Sairam RK, Srivastava GC and Saxena DC. 2000. Increased antioxidant activity under elevated temperatures: a mechanism of heat stress tolerance in wheat genotypes. *Biol Plant* **43**: 245-251.
- Sakata T and Higashitani A. 2008. Male sterility accompanied with abnormal anther development in plants genes and environmental stresses with special reference to high temperature injury. *Int J Plant Dev Biol* **2**: 42-51.
- Sharma KD and Pannu RK. 2007. Effect of heat stress on terminal stages of *B. juncea*. *J Oilseed Res* **24**: 267.
- Sharma P and Sardana V. 2012. Screening of Indian mustard (*B. juncea*) for thermo tolerance at seedling and terminal stage. *J Oilseed Brassica* **4**: 61-67.

- Singh M, Rathore SS and Raja P. 2014. Physiological and stress studies of different rapeseed- mustard genotypes under terminal heat stress. *Inter J G E Biotech* **5**:133-142.
- Takahama U .1996. Effects of fusicoccin and indole-3-acetic acid on the levels of ascorbic acid and dehydroascorbic acid in the apoplast during elongation of epicotyl segments of *Vigna angularis*. *Physiol Plant* **98**: 731-736.
- Tobias M and Niinemets U. 2005. Heat sensitivity of photosynthetic electron transport varies during the day due to changes in sugars and osmotic potential. *Plant Cell Environ* **29**: 212–218.
- Tyagi A, Santha IM and Mehta SL. 1999. Effect of water stress on proline content and transcript levels in *Lathyrus sativus*. *Ind J Biochem Biophy* **36**: 207-210.
- Van Camp W, Capiou K, Van Montaju M, Inze D and Slooten L. 1996. Enhancement of oxidative stress tolerance in transgenic tobacco plants over producing Fe-superoxide dismutase in chloroplasts. *Plant Physiol* **12**: 1703-1714.
- Wahid A and Close TJ. 2007. Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. *Biol Planta* **51**: 104-109.
- Wang W, Vinocur B and Altman A. 2003. Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. *Planta* **218**: 1-14.
- Wardlaw JF, Sofield I and Cartwright PM .1980. Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. *Aus J Plant Physiol* **7**: 387-400.
- Wilson RA, Sangha MK, Banga SS, Atwal AK and Gupta S. 2012. Heat stress tolerance in relation to oxidative stress and antioxidants in *B. juncea*. *J Environ Biol* **35**: 383-387.
- Wise RR. 1995. Chilling-enhanced photooxidation: The production, action and study of reactive oxygen species produced during chilling in the light. *Photo Res* **45**: 79-97.
- Xu S, Li J, Zhang X, Wei H and Cui L. 2006. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultra structure of chloroplasts in two cool-season turfgrass species under heat stress. *Environ Exp Bot* **56**: 274-285.
- Yadav S, Bhatia VS and Guruprasad KN. 2006. Oxyradical accumulation and their detoxification by ascorbic acid and a-tocopherol in soybean seeds during field weathering. *Ind J P Physiol* **11**: 28-35.
- Zhang Y, Wang L, Liu Y, Zhang Q, Wei Q and Zhang W. 2006. Nitric oxide enhances salt tolerance in maize seedlings through increasing activities of proton-pump and Na⁺/H⁺ antiport in the tonoplast. *Planta* **224**: 545-555.
- Zlatev Z and Lidon FC. 2012. An overview on drought induced changes in plant growth, water relations and photosynthesis. *Emirates J Food Agri* **24**: 57-72.