Interacting effects of high temperature and drought stresses in wheat genotypes under semiarid tropics- an appraisal

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ABSTRACT The production of wheat is one of the most important breeding targets in India. The major constraints in the productivity are based on the limiting usage of water. In this mini-review, the focus is on the physiological traits of wheat plants to obtain the tolerance against heat and drought stress. This will encourage the breeding program on wheat in semi arid tropics like India.

Key words: drought stress, India, water deficient, wheat

INTRODUCTION

Among different crop species wheat (*Triticum aestivum* L.) is one of the most important cultivated species. Yield potential of any variety is the combined effect of genotype and environmental interaction. Now a days global warming and scarcity of water are important factors for the wheat production throughout the world. In the last century, carbon dioxide concentration (CO₂) has risen rapidly from about 350 $\mu\text{mol mol}^{-1}$ in 1980 to about 378 $\mu\text{mol mol}^{-1}$ at present. At the current rate of gas emissions and population increase, it is predicted that CO₂ will double by end of this century. These changes in CO₂ and other greenhouse gases are predicted to increase surface mean temperature in the range of 1.4–5.8 °C. In addition, studies also show that in future climates will have more frequent short spells of high temperature (heat). Most crops are highly sensitive to heat stress and often result in progressively decreasing yields at temperatures above the optimum. Howard (1924) while analyzing the factors controlling wheat production remarked that “wheat production in India is a gamble in temperature”. This statement is valid even today. The cultivation of wheat is limited by abiotic stresses (moisture and temperature). The present day rice-wheat cropping

system and irregularities in monsoon have compelled wheat crop to face rapidly ascending temperatures coupled with moisture stress during the post-anthesis stages. These unfavorable environmental conditions severally affect post-anthesis stages and ultimately reduce yield considerably. It has already been established that stress due to high temperature can play significant role in reducing yield and quality of wheat (Stone and Nicolas, 1995). Wheat yields are reduced by 50–90 % of their irrigated potential by drought on at least 60 million ha in the developing world (Reynolds et al. 2001). Breeding for heat and moisture stress tolerance forms an integrated component of wheat breeding programme at both national and international level (Acevedo et al. 1990). One of the most important and economic ways to overcome negative effects of heat stress is to identify and/or develop heat-tolerant cultivars. At present, the major constraint for identifying heat-tolerant cultivars is the lack of reliable screening tool. Better understanding of the possible impact of high temperature stress on physiological, morphological, and yield processes would not only help in mitigating the adverse effects of high temperature stress but also in developing reliable field-screening tools (Singh et al. 2007). The present paper is an attempt to have an appraisal to understand the effects on morpho-physiological traits under high temperature and moisture stress conditions so that yield targets can be met out under changing conditions.

WATER RELATIONS

High temperature stress

Heat, as a stressor, adversely affects water status of the plant. Relative water content and excised leaf weight loss appeared to be one of the important characters as the varieties having better resistance also had better performance under high temperature and drought stress

(Dhanda and Sethi, 2004). High temperature and its effects on plant water relations were also reported by Machado and Paulsen (2001) and Deng Xi-Peng et al. (2005).

Drought

Relative water content has been reported as an important indicator of water stress in leaves, it closely reflects the balance between water supply to the leaf and transpiration rate (Lilley and Ludlow, 1996). This influences the ability of the plant to recover from stress which consequently affects yield and yield stability. Assessment of water loss from excised leaf weight loss has shown promise for characterizing drought resistance in wheat genotypes (Clarke, 1987; McCaig and Ramagosa, 1991). This trait is moderately heritable (Clarke and Towney-Smith, 1986) and can be easily determined in a large population (Dhanda and Sethi, 1998). Following excision, stomata close and after 20–30 min., the rate of water loss enters a linear phase that lasts for several hours (McCaig and Ramagosa, 1991). During this phase the water is lost from incompletely closed stomata. Sinclair and Ludlow (1986) noted that there is no conclusive proof that stomata of excised leaves are fully closed. Consequently, Clarke and Richards (1988) proposed to use the term residual transpiration, defined as the rate of water loss from excised leaves at minimum stomatal aperture, in place of cuticular transpiration. Excised leaf water loss was related to drought resistance in wheat (McCaig and Ramagosa, 1991; Dhanda et al. 1998), but its relationship was not consistent on various stages of plant growth (Dhanda, 1993; Dhanda et al. 1995). Recently, Dhanda et al. (2007) have reviewed wheat improvement under water deficit conditions in semi arid tropics and sub tropics.

High temperature and drought stresses

Shah (1992) reported that simultaneous heat and drought stresses reduced leaf water content, water potential and osmotic potential in wheat. Wheat and sorghum crops maintained nearly stable water relations regardless of temperature when moisture was ample, but high temperature strongly affected water relations when water was limiting. The combined stresses strongly reduced soil water content, leaf relative water content, leaf water potential and leaf osmotic potential (Machado and Paulsen, 2001).

The accumulation of proline in a variety of species under various kinds of stresses and its possible involvement in adaptive mechanisms has been reviewed by Aspinall and Paleg, (1981). Unlike the participation of proline and other free amino acids in the response to drought, their role during high temperature stress has not been studied so intensively. The protective role of proline during high temperature stress was shown in cotton, since cultivars with high proline content suffered less damage during heat stress (Ashraf et al. 1994). The involvement of free amino acids in response to heat stress was shown in spring wheat, where a mutant having greater amino acid contents (especially serine, methionine, histidine and arginine) was damaged to a lesser extent after heat stress treatment than the parent genotypes (Behl et al. 1991).

Drought

Free proline has been suggested as a metabolic measure of drought, and to play an important role as an organic osmolyte. Osmotic adjustment is an important acclimation mechanism which could allow for the maintenance of relatively greater metabolic functions at low leaf water potential (Laurie et al. 2002; Gilliam and Tester, 2005). An increasing number of reports provide evidence on the association between high rate of osmotic adjustment (OA) and sustained yield or biomass under water limited conditions across different cultivars of crop plants. Since OA helps to maintain higher leaf relative water content (RWC) at low leaf water potential (LWP), it is evident that OA helps to sustain growth while the plant is meeting transpirational demand by reducing its LWP. Osmotic adjustment is a major cellular stress adaptive response in certain crop plants that enhances dehydration avoidance and supports yield under stress (Blum, 2005). Nayyar and Walia (2003) demonstrated adaptive role of proline during drought stress. They observed a higher rate of proline accumulation and utilization during water-deficit in a drought tolerant wheat genotype C 306 compared to a drought sensitive HD 2380. The involvement of proline in the response to water shortage was also demonstrated in transgenic tobacco over expressing an enzyme of proline biosynthesis, ornithine amino- Δ -aminotransferase. These transgenic plants exhibited higher proline levels and improved drought tolerance (Roosens et al. 2002). An increase in the content of proline in leaves of transgenic potato lines was noticed under water stress by Knipp and Honermeier (2006).

PROLINE

High temperature stress

High temperature and drought stresses

The effect of simultaneous drought and heat stress on

free amino acid level was compared in wild type and transgenic soybean plants transformed with cDNA coding for the last enzyme of proline biosynthesis, L- Δ^1 -pyrroline-5-carboxylate reductase, in sense and antisense direction. The most rapid increase in proline content was found in the sense transformants that exhibited the least water loss, while the slowest elevation of proline levels was detected in the antisense transformants that exhibited the greatest water loss during stress (Simon-Sarkadi et al. 2005).

PHOTOSYNTHESIS

High temperature stress

Net photosynthesis is reversibly inhibited at moderately higher temperature. Photosynthetic pigment composition and photosystem II (PS II) photochemistry gets altered during high temperature stress period. During leaf senescence, neoxanthin and β -carotene decreased concomitantly with chlorophyll, whereas lutein and xanthophyll cycle pigments were less affected. The chlorophyll a/b ratio also increased (Lu et al. 2001). Photosynthetic rates and thylakoid activities are adversely affected by high temperatures in wheat (Al-Khatib and Paulsen, 1990). The photosynthetic response to high temperature included adverse association with light reactions and injury to PS II in wheat (Havaux, 1992). Recent research has shown significant variation among wheat cultivars with respect to reduction in photosynthesis at high temperature. Genotypes most tolerant to high temperatures had the most stable leaf photosynthetic rates or had longer duration of leaf photosynthetic activity after anthesis (Abrol and Ingram, 1996). High temperature enhanced light harvesting complex (LHC II) phosphorylation either because of activation of kinase or by suppression of phosphatase activity. The induced ability of LHC II for enhanced phosphorylation may enable better energy distribution in favour of photosystem I (PS I) (Satpathy and Mohanty, 2000). High temperature is known to influence the migration of LHC II (Mohanty and Vani, 2003). High temperature impacts plant biomass accumulation by altering the rate of net photosynthesis due to limiting activity of ribulose 1, 5 biphosphate carboxylase/oxygenase (Rubisco). The activation state of Rubisco, which is regulated by the activity of Rubisco activase, appears to be primary limitation to net photosynthesis at high temperature (Salvucci and Crafts-Brandner, 2004a). ATP pools were speculated to be compensated by increased cyclic phosphorylation by PS I or lowered

usage of ATP due to deactivation of Rubisco (Salvucci and Crafts-Brandner, 2004b). High temperature decreased wheat productivity by adversely affecting photosynthetic rate and viable leaf area during maturation (Shah and Paulsen, 2005). Heat stress decreased chlorophyll content and net photosynthetic rate (Morales et al. 2003; Todorov et al. 2003). Decrease in chlorophyll content, ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) binding protein, Rubisco activase was investigated in wheat leaf segments during heat stress (Demirevska-Kepova et al. 2005).

Drought

Water stress is one of the important environmental factors inhibiting the process of photosynthesis. In particular, PS II photochemistry has been shown to be very sensitive to water stress (Masojidek et al. 1991; Van Rensburg and Kruger, 1993). Several *in vivo* studies demonstrated that water stress damaged the oxygen evolving complex of PS II (Toivonen and Vidaver, 1988) and to the PS II reaction centres (Havaux et al. 1986, 1987). It seems such damage to PS II reaction centers was associated with the degradation of D1 protein (He et al. 1995; Giardi et al. 1996). Liang et al. (1997) have shown that drought induced decrease of photosynthesis was mainly a result of the closure of stomata caused by the increased amino butyric acid concentration in the xylem. Exposure of plants to drought led to noticeable decrease in photosynthesis rate, stomatal and mesophyll conductance and a concomitant increase in intercellular CO₂ concentration (Siddique et al. 1999). Water deficit at vegetative and anthesis stage significantly reduced net photosynthesis. Stress induced reductions in photosynthetic rate were found to be up to 65 % and 80 % for vegetative and anthesis drought, respectively (Brar et al. 1990). Water deficit along with nitrogen deficiency strongly reduced the photosynthetic activity by decreasing the efficiency of PS II and efficiency of potential photosynthetic quantum conversions of leaves significantly (Shangguan et al. 2000). Severe drought significantly reduced photosynthesis, shoot and root biomass and root respiration rate (Liu and Li, 2005).

High temperature and drought stresses

Heat and drought stress decreased photosynthetic rate, however, the decline in photosynthetic rate was more severe under heat than under drought stress during the first 12 days of treatment in Kentucky blue grass. The combined heat and drought stresses caused more dramatic reductions in photosynthetic rate than either

heat or drought alone (Jiang and Huang, 2000). Drought decreased photosynthetic rate and high temperature hastened the decline in photosynthetic rate in wheat. Interactions between the two stresses were pronounced, and consequences of drought on all physiological parameters were more severe at high temperature than low temperature. The synergistic interactions indicated that productivity of wheat is reduced considerably more by the combined stress than by either stress alone, and much of the effect is on photosynthetic processes (Shah and Paulsen, 2003). Photosynthesis and its tolerance to photo-inhibition and high temperature and drought stress of flag leaves were investigated in wheat (*Triticum aestivum* L.) hybridization line (1-12) and its parents (Jing-411 and Xiaoyan-54). To characterize photo-oxidative damage, tolerance to photo-inhibition, high temperature and drought stress was compared in 1-12 and its parents. When exposed to high light ($1400 \mu\text{mol m}^{-2} \text{s}^{-1}$), the maximal efficiency of PS II photochemistry (Fv/Fm) decreased significantly with increasing exposure time and such a decrease was much less in 1-12 than in its parents. When exposed to higher temperatures (30–45 °C) for 15 min., Fv/Fm started to decrease at 42 °C in 1-12 and its parents. The greatest decrease in Fv/Fm was observed in Jing-411. 1-12 and Xiaoyan-54 showed a comparable decrease in Fv/Fm. Similar results were also observed in the actual PS II efficiency ($\Phi \text{PS II}$), photochemical quenching (qP) and non-photochemical quenching (qN). During exposure of detached leaves to air under room temperature conditions, relative water content decreased with increasing exposure time. However, such a decrease was the greatest in Jing-411 followed by Xiaoyan-54, and 1-12. In addition, the activities of ribulose-1, 5-bisphosphate carboxylase, phosphoenolpyruvate carboxylase, pyruvate phosphate dikinase, NADP-malate dehydrogenase and NADP-malate enzyme were significantly higher in 1-12 than in its parents. The results obtained in this study suggested that high resistance to photo-oxidative damage of the flag leaves in 1-12 may be the physiological basis for its high yield when grown in north China (Yang et al. 2006).

TRANSPIRATION AND STOMATAL CONDUCTANCE

High temperature stress

A rise in temperature due to green house effect tends to stimulation of transpiration. Evaporative demand exhibits near exponential increase with increase in daytime temperature and results in high transpiration

rates and low plant water potential (Hall, 2001). Change in vapor pressure deficit at leaf surface tends to increase transpiration at higher temperatures. High temperature was found to correlate strongly with stomatal conductance and grain yield (Rekika et al. 2000). Partial stomatal closure at high temperature alleviates water stress during period of high water requirement (Geijn and Goudrian, 1996). Stomatal closure lessens the stomatal gas exchange at higher temperatures. The adaptive advantage of higher stomatal conductance appears to be associated with leaf cooling (Munjal and Dhanda, 2004). Thus stomatal conductance could be valuable selection criteria for higher yields in wheat grown at supra-optimal temperatures (Zhenmin et al. 1998).

Drought

Water stress may increase pH of the xylem sap before it reaches the leaves, thus it may be able to cause an increase of the apoplastic pH which may further induce stomatal closure (Slovic and Hartung, 1992). Backcrossing genotypes with superior transpiration efficiency into locally adapted cultivars have shown 10 per cent better yield at water limited site (Turner, 1997). Drought induced root borne signals probably control stomatal conductance and leaf extension rate during mild soil drying in the field (Ali et al. 1998).

High temperature and drought stresses

High temperature and drought often occur simultaneously, but their effects on crops have been usually investigated individually. Drought decreased stomatal conductance, viable leaf area, photosynthesis, shoot and grain mass and weight but increased plant water use efficiency in wheat. High temperature hastened the decline in photosynthesis and leaf area, decreased shoot and grain mass as well as weight and reduced water use efficiency. The interactions between the two stresses were pronounced and simultaneous drought and heat stress were more detrimental than either stress alone (Shah and Paulsen, 2005). Drought preconditioned plants maintained higher stomatal conductance, transpiration rate and photosynthesis than non-preconditioned plants during subsequent heat stress in turfgrass (Jiang and Huang, 2000).

MEMBRANE THERMOSTABILITY

High temperature stress

Thermostability of various cellular membranes is important during high temperature stress. Excessive

fluidity of membranes due to high temperature is associated with loss of physiological functions. High temperature stress leads to increased membrane permeability and hence increased ion and solute flux (Levitt, 1980). Membrane thermostability is an important index of screening cultivars for thermo-tolerance (Blum and Ebercon, 1981; Munjal et al. 2004). Adaptations of plants to high temperature are because of functional cell membrane system during heat stress. Membrane thermostability of durum wheat is significantly greater than that of bread wheat (Galiba et al. 1997). Temperature above 30 °C causes disorientation of lamellar structure of chloroplast. Increased activity of hydrolytic enzymes promotes the rate of ion transport under heat stress conditions (Singla et al. 1997). Plants have evolved a variety of responses to elevated temperatures that minimize damage and ensure protection of cellular homeostasis. New information about the structure and function of heat stress proteins and molecular chaperones has become available. At the same time, transcriptome analysis of *Arabidopsis* has revealed the involvement of factors other than classical heat stress responsive genes in thermotolerance. Recent reports suggest that both plant hormones and reactive oxygen species also contribute to heat stress signaling. Additionally, an increasing number of mutants that have altered thermotolerance have extended our understanding of the complexity of the heat stress response in plants (Kotak et al. 2007). Thermo-tolerant wheat lines have higher membrane thermostability, lower internal CO₂ concentration and higher rates of dark respiration than the susceptible ones (Reynolds et al. 1998). High temperature stress leads to loss of membrane integrity followed by increase in cell permeability (Taiz and Zeiger, 2002). Membrane thermostability is one of the important parameter and indicates genetic variability for heat stress (Craufurd et al. 2003).

Membrane lipid saturation is considered an important element in high temperature tolerance. In mutant wheat line with increased heat resistance, heat treatment increased relative quantities of linolenic acid among galactolipids and trans- Δ^3 hexadecanoic acid among phospholipids compared with wild type wheat plants (Behl et al. 1996). Severe heat stress caused denaturation of membrane proteins and melting of membrane lipids which cause membrane rupture and loss of cellular contents (Abrol and Ingram, 1996). Heat tolerance based on membrane thermostability is a valuable supplementary criterion in final breeding stage or as a rough selection tool to reduce large population

into heat tolerant core at early stages of breeding programme (Blum et al. 2001).

Drought

Bewley (1979) emphasized the critical role of cell membrane stability under conditions of moisture stress as a major component of drought tolerance. Cell membrane stability under water stress can be of possible adaptive value and indicative of drought stress tolerance (Krishnamani et al. 1984). Under extreme dehydration stress, membranes undergo a degradative process, leading to a buildup of conjugated lipids such as triglycerides, sterol esters and sterol glucosides. Water stress resulted in reduction of about 24 and 31 % in total lipids and phospholipids in plasma membrane, respectively. Also the amount of glycolipids and diacylglycerols decreased significantly upon water stress (Navari-Izzo et al. 1993). Associations between osmotic adjustment and cellular membrane stability under drought stress were suggested more recently (Chandra Babu et al. 2004).

High temperature and drought stresses

Simultaneous heat and drought stress increased cell membrane permeability of perennial ryegrass (Chen et al. 1988). The interaction of heat and drought caused more rapid and severe damage of cell membrane stability than either stress alone.

STEM RESERVE MOBILISATION

High temperature stress

Stored stem reserves serve as a source of carbon for grain filling in wheat, particularly during stress conditions. The grain filling of wheat is seriously impaired by heat stress due to reductions in current leaf and ear photosynthates at high temperatures. An alternative source of carbon for grain filling is stored stem reserves. Stem may play an important role when assimilates accumulate in stem and later on retranslocate, because it may maintain reproductive growth under stress conditions (Blum et al. 1994). In wheat, peduncle and penultimate internode contained more reserve storage (Wardlaw and Willenbrink, 1994). Dry matter loss from the second internode during grain filling positively correlated with yield, mass per grain, number and mass of grains per ear and harvest index. By contrast, dry matter loss was negatively correlated with relative growth rate of main shoots during grain filling and means temperature from sowing to anthesis (Cruz-Aguado et al. 2000).

Greater stem reserve mobilization in tolerant wheat genotypes supported grain filling during critical stage of dry matter accumulation in grain and helped in providing tolerance to post-anthesis heat stress (Shukla et al. 1997). Thermo-tolerant wheat genotypes CBW 12 and NIAW 845 showed lesser reduction in grain weight (12 %) whereas more than 30 % reduction in grain weight was observed in thermo-susceptible genotypes viz. Raj 4014 and HUW 510, conferring the role of stem reserves in grain filling. This was further supported by close association between contribution of stem reserve for grain development and depletion of soluble sugars in stem at harvest (Rane et al. 2003). The demand by grain sink was the primary factor in determining stem reserve mobilization. The interaction between ear size and demand for stem storage appeared to depend upon the environment before or during grain filling (Bonett and Incoll, 1992). The rate of stem reserve mobilization was not sufficiently high to compensate for reduction in grain filling duration at high temperature (Blum, 1998).

Drought

Yang et al. (2001) reported that 75–92 % of pre-anthesis ¹⁴C stored in the straw was reallocated to grains of wheat cultivar, Yangmai 158 and Yangmai 931 in water-deficit treatments, 50 to 80 % higher than the amount in well-watered treatments, indicating that water deficits promoted remobilization. Internode length, weight and specific weight were reduced under drought. Drought increased mobilization efficiency, expressed as percentage of maximum dry matter mobilized, in the peduncle, penultimate and the lower internodes by 65, 11 and 5 %, respectively in wheat (Ehdaie et al. 2006).

High temperature and drought stresses

Jiang and Huang (2000) reported that drought or heat alone, or heat and drought, significantly reduced root dry weight in Kentucky blue grass. However, reduction was more severe under heat alone than under drought stress. Drought preconditioning significantly increased root dry weight as compared to non-preconditioned plants during subsequent heat stress. Simultaneous drought and heat stresses were more detrimental than either stress alone.

CONCLUSIONS

The wheat crop is grown in diverse agro-ecological conditions ranging from temperate to subtropical climates. Thus, considerable climatic differences in temperature and relative humidity exist in these areas

and wheat crop experiences wide seasonal variations. High temperature hastened the decline in photosynthetic rate and viable leaf area during maturation, decreased relative water content and reduced water use efficiency. Drought increased stomatal resistance, decreased photosynthesis and enhanced water use efficiency. Recent research has shown significant variation among wheat cultivars with respect to reduction in photosynthesis at high temperature. Genotypes most tolerant to high temperatures had the most stable leaf photosynthetic rates or had longer duration of leaf photosynthetic activity after anthesis. However, high photosynthetic rates at high temperature do not necessarily support high rates of dry matter accumulation. Interactions between the two stresses were pronounced and consequences of drought on all physiological parameters were more severe at high temperature than low temperature. The synergistic interactions indicated that productivity of wheat is reduced considerably more by the combined stress than by either stress alone. Simultaneous drought and heat stresses were more detrimental than either stress alone. High-temperature stresses affects all growth stages of crops and ultimately yields. This is further aggravated by other environmental stresses like intermittent drought and high light. Management options are few and hence developing intrinsically tolerant plants is essential to combat the situation. As thermotolerance is a multigenic trait, emphasis needs to be on relevant approaches to assess genetic variability in basal and acquired tolerance. This is in fact the major aspect in crop improvement programmes (Senthil-Kumar et al. 2007). Breeding for abiotic (thermo and moisture) stress tolerance in wheat cultivars requires understanding of the physiological responses of wheat crop to these stresses, which will help in identifying traits, to be used as selection criteria.

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Received 8th Nov. 2007Accepted 23rd Jan. 2008