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Effects of High Night Temperature on Crop Physiology and Productivity: Plant Growth Regulators Provide a Management Option

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1. Introduction

Crop production is experiencing both increases in the frequency and intensity of high night temperatures (HNT) (IPCC, 2007). The HNT threatens the sustainability of crop production both currently and in the future. Recent meteorological data indicated faster increases in night temperatures (NT) than day temperatures (Alward et al., 1999). Experimental evidence also indicated the importance of assessing the effects of NT separately from the day temperature, as a smaller increase in NT can show a drastic decrease in crop production (Peng et al., 2004). Studies have indicated decreased crop yields as a result of HNT (Hall, 1992; Mohammed & Tarpley, 2009a). Apart from HNT, climate change will also increase a variety of environmental stresses affecting crop production, namely heat, drought, salinity, and relative humidity, hence farming in the future climate will have to be better adapted to a range of abiotic and biotic stresses. A long-term approach to negate the effects of abiotic stress is to develop stress-tolerant cultivars. The short-term approach includes the use of agrochemicals, especially those with plant growth regulator (PGR) capabilities, for the prevention and/or amelioration of various environmental stresses, including heat stress. Studies focusing on day temperature stress and, more recently, on NT stress have increased, but, studies looking at the effects of PGR under heat stress are rare (Ashraf & Foolad, 2007). This chapter primarily focuses on the effects of HNT on crop production and the beneficial effects of PGR (glycine betaine [GB] and salicylic acid [SA]) application against heat stress on crop production with special emphasis on rice (*Oryza sativa* L.) production.

2. Night temperature and its impact on crop production

Global climate change is a dynamic process affecting global air temperature, oceanic temperature, rainfall, wind and quality of incoming solar radiation. Global circulation models predict 1.4 to 5.8 °C rise in global temperature because of projected increase in the concentrations of all greenhouse gases by the end of the 21st century (Intergovernmental Panel on Climate Change [IPCC], 2007). Much of this increase in average daily temperature is projected to be due to an increase in NT. Night temperatures are expected to increase at a faster rate than day temperatures due to less radiant heat loss because of increased

cloudiness (Alward et al., 1999). In some cases, increases in NT have been documented. For example, the scientists at the International Rice Research Institute (IRRI) reported an increase of 1.13 °C in NT over a period of 25 years (1979-2003) in the Philippines (Peng et al., 2004). The HNT increased at a rate of 0.18 °C per decade over a period of 45 years (1950-1995) in Libya (Jones et al., 1999).

Long- and short-term episodes of heat stress are predicted to occur more frequently as a result of global warming, affecting many aspects of crop growth and development, reducing crop yield and decreasing crop quality. Many studies have reported the impacts of long- and short-term temperature stresses on crop production. However, most of the studies assume no difference in the influence of day versus night temperature (Peng et al., 2004). High night temperature is known to decrease yield in several crops like cereals [rice, wheat (*Triticum aestivum* L.) and corn (*Zea Mays* L.)], legumes [cowpea (*Vigna unguiculata* L. Walp.)], oil seeds [soybean (*Glycine max* L. Merr.) and sunflower (*Helianthus annuus L.*), vegetables [tomato (*Solanum lycopersicum* L.)], fruits [apples (*Malus domestica* L.) and pineapple (*Ananas comosus* L.)] and fibers [cotton (*Gossypium hirsutum* L.)] (Chang, 1981; Gibson & Mullen, 1996; Izquierdo et al., 2002; Kondo & Takahashi, 1989; Loka & Oosterhuis, 2010; Mohammed & Tarpley, 2009a; Neales et al., 1980; Peters et al., 1971; Seddigh & Jolliff, 1984; Warrag & Hall, 1984; Willits & Peet, 1998).

High night temperature decreases crop production by decreasing photosynthetic function, sugar and starch content (Loka & Oosterhuis, 2010; Turnbull et al., 2002), increasing respiration rate (Mohammed & Tarpley, 2009b), suppressing floral bud development (Ahmed & Hall, 1993), causing male sterility and low pollen viability and hastening crop maturity (Mohammed & Tarpley, 2009a; Seddigh and Jolliff, 1984). Another effect of HNT that can contribute to reduced crop yield is decreased antioxidant capacity of the plants. Under normal physiological conditions, the toxic effects of reactive oxygen species (ROS) are minimized by enzymatic and non-enzymatic antioxidants. Under stress conditions, oxidant levels can overwhelm the antioxidant levels leading to cell damage. The increased production of ROS [oxide radical (O_2^-), H_2O_2, and the hydroxyl radical (-OH)], or the plant's decreased ability to neutralize ROS, as a result of heat stress negatively affects many physiological processes in plants, thus decreasing yield.

2.1 Methodology for determining rice plant response to high night temperature stress

Plant height and the numbers of tillers and leaves were recorded at harvest. Daily observations were made for the appearance of panicles. At harvest, leaves were separated from the stems and leaf area was measured using a CI-251 area meter (CID Inc., Camas, Washington, USA). During the rice plant vegetative stage, leaf photosynthetic rate, internal CO_2 concentration and respiration rate were measured using LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA). Leaf nitrogen content was determined using a FP-528 Nitrogen/Protein analyzer (LECO Corporation, St. Joseph, Michigan, USA) and was expressed as percentage (%; w/w). Total chlorophyll content, pollen germination and spikelet fertility were determined using the procedures from Mohammed & Tarpley (2011a), and relative injury to the membrane and total antioxidant capacity were determined using procedures from Mohammed & Tarpley (2009b).

2.2 Effects of high night temperature on plant morphology

Plant morphology deals with plant development, form, and structure. In a narrow sense, plant morphology refers to the external appearance of the plant. For example plant height

and the numbers of tillers, leaves, panicles and grains are referred as rice morphological parameters. The effects of HNT on plant morphology vary from negative to positive, including no effect. Seddigh & Jolliff (1984) reported that HNT promoted early vegetative growth and hastened physiological maturity, but did not affect morphological characteristics such as plant height, number of auxiliary branches and number of nodes in soybean. The HNT has no effect on rice (cultivar Cocodrie which is a japonica cultivar) plant height and number of tillers but can increase number of leaves and leaf area (Fig. 1). However, Cheng et al. (2009) and Yoshida et al. (1981) reported reduction in plant height, number of tillers and total biomass for rice cultivar 'IR 72' (indica cultivar) as a result of HNT. Similar results were seen in redstem stork's bill (*Erodium cicutarium* L.) for which HNT decreased number of branches, leaf area and plant dry matter (Blackshaw & Entz, 1995). The decreased production of plant dry matter was directly correlated with decreased production of photosynthates.

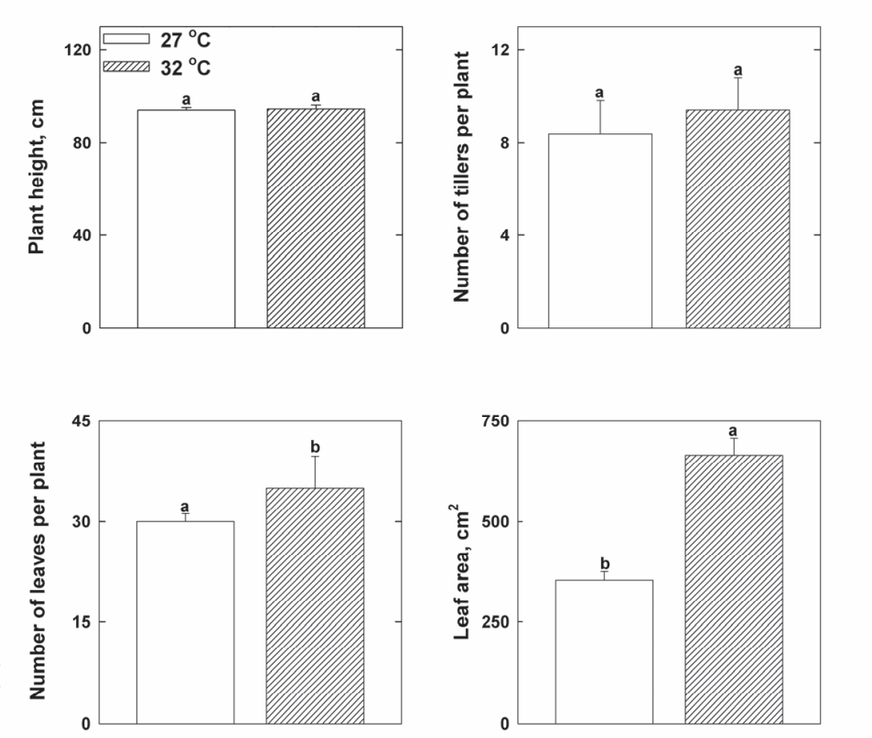


Fig. 1. Effects of high night temperature on rice morphology. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

2.3 Effects of high night temperature on plant physiology

Plant physiology deals with the functioning of plants and is closely related with plant morphology. Fundamental processes such as photosynthesis, respiration, plant water and nutrition status, plant hormone functions and translocation of photosynthates are encompassed in plant physiology. Photosynthesis is a complex process and leaf photosynthetic rates depend upon leaf chlorophyll and nitrogen content, photosystems, stomatal characteristics and enzyme activities. The environmental stresses have a direct effect on leaf photosynthetic rates and an indirect effect through their effects on leaf

chlorophyll and nitrogen content, stomatal characteristics and enzyme activities. The HNT had positive and negative effects, including no effect, on the following day's photosynthetic rates (Frantz et al., 2004; Mohammed & Tarpley 2009a). Rice leaf photosynthetic rates showed negative correlation with HNT (Fig. 2). The decrease in photosynthetic rates as a result of HNT was accompanied with decrease in leaf chlorophyll and leaf nitrogen content in rice (Fig. 2). Premature loss of chlorophyll as a result of heat stress has been noticed in many crop species (Guo et al., 2006; Reynolds et al., 1994). Damage to the photosynthetic electron transport particularly at the site of photosystem II (Havaux and Tardy, 1996) and inhibition of photosynthetic CO_2 fixation (Sayed et al., 1989; Yamane et al., 1997) as a result of heat stress can also reduce photosynthetic rates, thus leading to decrease in yield. Apart from decreases in photosynthetic rates, increased respiration rates can also decrease the crop yield.

Plant respiration is one of the important processes in terms of understanding plant growth and development when subjected to stress. Increase in respiration from climate warming is of serious concern as respiratory processes can consume a larger portion of total photosynthates (Paembonan et al., 1992). On average, the carbon lost from respiratory metabolism within an individual plant ranges between 30 and 70% of the carbon gained through photosynthesis (Peterson & Zelitch, 1982). Respiration is typically partitioned into the functional components of construction (growth), maintenance and ion uptake to facilitate our understanding of the impact of the environment on respiratory processes (Amthor, 1986; Farrar, 1985; Lambers, 1985). Maintenance respiration is mainly associated with turnover of proteins and lipids and maintenance of ion concentrations across membranes (Penning de Vries, 1975). It is the most responsive to environmental changes among the functional components of respiration (Ryan, 1991). At high temperatures, the cost of maintenance increases to support protein turnover and to maintain active ion fluxes across the membranes (Penning de Vries, 1975), thereby increasing maintenance respiration. An increase in NT from 27 ^{o}C to 32 ^{o}C increased respiration rates by 40% in rice leaves (Fig. 2). Previous studies on rice, cotton, lettuce (*Lactuca sativa* L.), tomato and soybean indicated an increase in maintenance respiration with warmer nights (Frantz et al., 2004; Loka & Oosterhuis, 2010, Mohammed & Tarpley, 2009b). Hence, HNT can stimulate respiration rates, thereby negatively affecting the yield (Zheng et al., 2002). The other consequence of increased respiration is increased production of ROS.

The production of ROS is an unavoidable consequence of aerobic respiration, with the majority of the ROS produced in photosynthetic tissue (mostly leaves) in the dark by mitochondrial electron transport chain activity (miETC) (McDonald & Vanlerberghe, 2005). The production of ROS by mitochondria has been shown to increase in many plants as a result of biotic and abiotic stresses (McDonald & Vanlerberghe, 2005; Moller, 2001). An increase in NT increases maintenance respiration and thus increases production of ROS. Physiological injury due to heat stress has been associated with increases in oxidative damage to the membrane in plant species (Larkindale & Knight, 2002). Plants increase maintenance respiration to support repair mechanisms of the membranes due to oxidative damage (Amthor & McCree, 1990). Thus, an increase in respiration occurs 1) with an increase in temperature (Huang et al., 1998) and 2) to support repair mechanisms of the membranes due to oxidative damage (Amthor & McCree, 1990). In addition, ROS interferes with photosynthesis and respiration by disrupting water, ion, and organic solute movement across plant membranes by affecting membrane stability (Christiansen, 1978).

Destabilized membranes are leaky membranes, thus interpreting the amount of electrolytic leakage from the membrane can be used as an indicator of cell membrane stability (Sullivan & Ross, 1979). Many studies have examined stability loss of the membranes subjected to environmental stresses by measuring electrolytic leakage from the membranes (Blum & Ebrercon, 1981; Dexter, 1956; Ibrahim and Quick, 2001; Ismail and Hall, 1999; Sullivan, 1972). An increase in NT from 27 ^{o}C to 32 ^{o}C increased injury to the membrane by 60% in rice leaves (Fig. 2). Similar results of increased injury to the membrane as a result of heat stress were seen in many crop species (Ibrahim & Quick, 2001; Ismail & Hall, 1999;, Martineau et al., 1979; Mohammed & Tarpley, 2009b). The properties of the photosynthetic system, including key enzymes and thylakoid membrane activities depend on the stability of membranes (Björkman et al., 1980). Moreover, it is well known that a functional cell-membrane system is central to crop productivity and acclimation of plants to high temperature (Raison et al., 1980). Mohammed & Tarpley (2009b) and Reynolds et al. (1994) positively associated membrane stability with yield performance under heat-stressed conditions in rice and wheat.

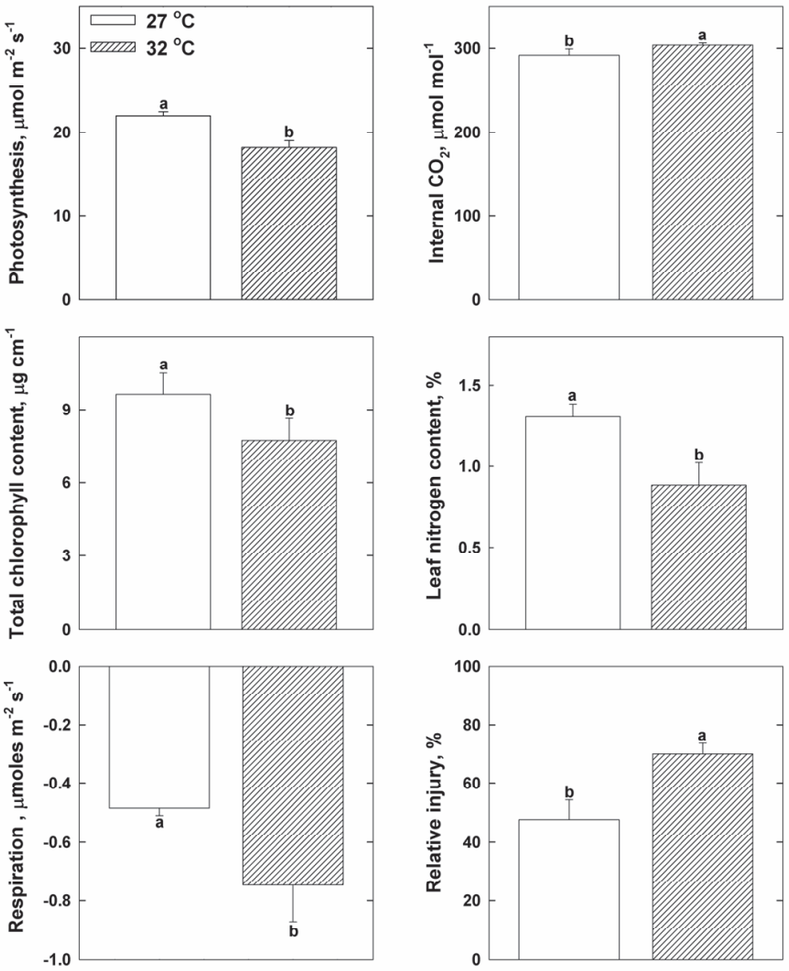


Fig. 2. Effects of high night temperature on rice physiology. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

2.4 Effects of high night temperature on yield and yield-related parameters

The reproductive phase is relatively more sensitive than the vegetative phase to heat stress in many crop species (Hall, 1992). Moreover, differential temperature sensitivity for reproductive and vegetative growth has been reported in rice (Baker et al., 1992), soybean (Baker et al., 1989), wheat (Mitchell et al., 1993) and many other crops. Warrag & Hall (1984) reported that HNT induced male sterility and excessive floral abscissions in cowpea, whereas high day temperature had no adverse effect. The HNT can decrease crop yields by decreasing crop growth duration, suppressing floral bud development and decreasing pollen production and viability (Ahmed & Hall, 1993; Mohammed & Tarpley, 2009a; Prasad et al., 1999; Prasad et al., 2006). Increase in NT from 27 ^{o}C to 32 ^{o}C decreased crop growth duration by 2 days, as indicated by emergence of 1st panicle, in rice (Fig. 3). Decreased crop duration due to HNT decreases the time for carbohydrate accumulation, thus decreasing the yield (Cantarero et al., 1999). Badu-Apraku et al. (1983) attributed dramatic yield loss under high temperatures during the period of grain filling to sucrose availability (Afuakwa et al., 1984) and activity levels of enzymes involved in starch and sugar metabolism (Singletary et al., 1994). Moreover, the suppression of floral buds and flowering under HNT was also attributed to a shortage of photosynthetic assimilates supplied to the floral buds (Guinn, 1974), and/or an inability of floral buds to mobilize carbohydrates under heat stress (Dinar & Rudich, 1985). Decreased pollen germination due to heat stress has been noticed in many crop species (Hall, 1992; Matsui et al., 2001; Mohammed & Tarpley, 2009a). This decrease in pollen germination at high temperatures is due to poor anther dehiscence and pollen reception (Prasad et al., 2006), reduced pollen swelling and decreased anther pore size (Matsui & Kagata, 2003).

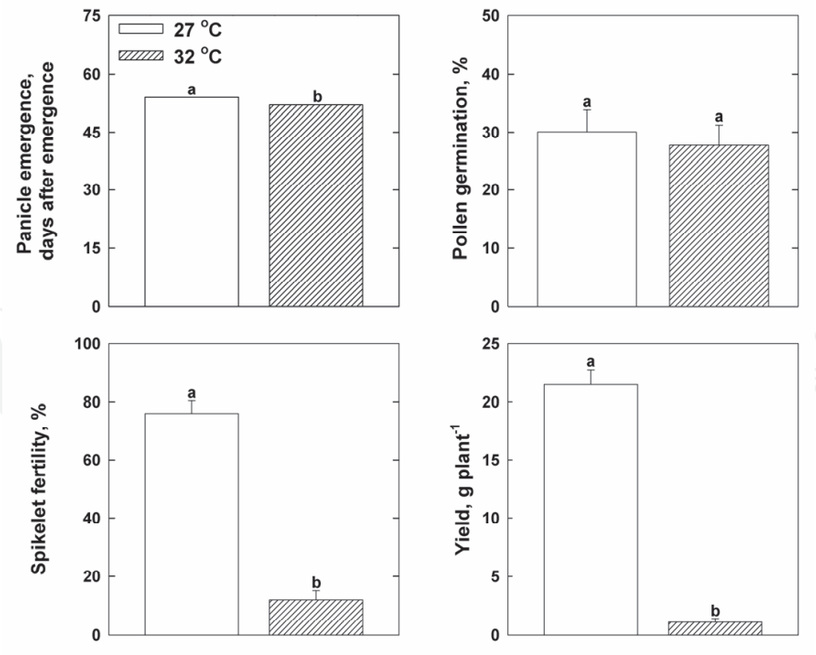


Fig. 3. Effects of high night temperature on rice yield-related parameters. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

In most cereal crops, spikelet fertility, described as the ratio between filled grains and total grains, decreased with decrease in pollen germination. Increase in NT from 27 ^{o}C to 32 ^{o}C decreased spikelet fertility by 70% in rice (Fig. 3). Apart from pollen germination, hormonal balance in the sink (Micheal & Beringer, 1980) and/or availability and transportability of photosynthates to the sink from the source (Afuakwa et al., 1984) and/or inability of floral buds to mobilize carbohydrates (Dinar & Rudich, 1985) and/or altered activities of starch and sugar biosynthesis enzymes (Keeling et al., 1994; Singletary et al., 1994) can govern the spikelet fertility at high temperatures. The capacity to survive heat stress varies with plant species, genotype and developmental stage. The PGR provide an option to protect the plants from heat stress, thus providing sustainability for crop productivity.

3. Plant growth regulators

Genetic improvement and the modification of agronomic practices can be beneficial for crop adaptation to future climate conditions. However, these approaches are more applicable for long-term episodes of heat stress. The use of agrochemicals, especially those with PGR capabilities, for the prevention and/or amelioration of various environmental stresses, such as those resulting from global climatic change, is a viable approach to make crop production more resilient to short-term episodes of heat stress. Plant growth regulators are natural or synthetic chemical compounds that are used to promote or inhibit plant growth and development or alter specific physiology or metabolic factors. Like plant hormones, small concentrations of PGRs are enough to influence plant growth and development. In recent years, numerous PGRs have been developed to promote crop production under stress conditions. Glycine betaine, SA, vitamin E, proline and choline are some of the agrochemicals which can induce stress-tolerance (thermotolerance, drought tolerance, cold tolerance and/or salinity tolerance) in various crop plants. In this chapter, we focus on the beneficial effects of GB and SA application against heat stress on crop production.

Oxygen is potentially toxic to all organisms because metabolism and environmental stresses generate ROS from the oxygen. Under normal physiological conditions, the toxic effects of ROS are minimized by enzymatic and non-enzymatic antioxidants (Kreiner et al., 2002). Under stress conditions, oxidant levels overwhelm the antioxidant levels leading to cell damage (Kreiner et al., 2002). Plants exposed to environmental stress, such as heat, cold, drought and salinity produce ROS, which damage macromolecules and cell membranes (Zhang & Kirkham, 1996). Angiosperms possess several enzymatic and non-enzymatic scavenging systems to minimize deleterious effects of ROS. These include lipid-soluble antioxidants (e.g. α-tocopherol and β-carotene), water-soluble reactants (e.g. ascorbic acid and glutathione), and enzymatic antioxidants (e.g. superoxide dismutase, catalase and enzymes of the ascorbate and glutathione cycle) (Zhang & Kirkham, 1996). Glycine betaine and SA are synthesized in the plants and play important but different, roles in preventing oxidative damage to the membranes (Bowler et al., 1992; Demiral & Turkan, 2004) and inducing theromotolerance in plants subjected to stresses (Ashraf & Foolad, 2007; Caldas et al., 1999; Farooq et al., 2008a, 2008b; Larkindale & Huang, 2004; Mohammed & Tarpley, 2009b; Pan et al., 2006; Raskin, 1992). The commercial availability of GB and SA provides potential crop-management options to reduce crop heat stress events.

Glycine betaine, an important osmoprotectant is an amino-acid derivative that is naturally synthesized and accumulates under stress conditions in some plants (Bohnert & Jensen, 1996; Demiral & Turkan, 2004). It enhances stress tolerance by protecting enzymes (Paleg et

al., 1981), photosystem II (Allakhverdiev et al., 1996), membrane integrity and antioxidant status of the plant (Mohammed & Tarpley, 2009b). Glycine betaine may also protect plants from environmental stresses indirectly via its role in signal transduction and ion homeostasis (John, 2002; Yilmaz, 2004). It regulates signal transduction and ion homeostasis by affecting MAP kinases, and expression of many genes related to signal transduction (John, 2002). Exogenous application of GB improved growth, survival and induced stress tolerance in many crop species (Diaz-Zorita et al., 2001; Harinasut et al., 1996; Rajasekaran et al., 1997) and also increased total antioxidant capacity and antioxidant enzyme activities (Farooq et al., 2008a; Mohammed & Tarpley, 2009b).

Salicylic acid is an endogenous plant growth regulator of phenolic nature and is considered to be a potent plant hormone because of its diverse regulatory roles in plant metabolism (Raskin, 1992). It plays an important role in the regulation of plant growth, development and responses to abiotic and biotic stresses (Raskin, 1992; Senaratna et al., 2000; Yalpani et al., 1994) by affecting photosynthetic rate, stomatal conductance, transpiration, ion uptake and transport, respiration rates, membrane stability, antioxidant capacity and antioxidant enzyme activities (Farooq et al., 2008a; Harper & Balke, 1981; Khan et al., 2003; Mohammed & Tarpley, 2009b). In addition, SA is considered to be an important signaling molecule involved in stress tolerance. It also promotes pathogenisis-related (PR) gene expression and induces systemic acquired resistance (SAR) in plants (Ryals et al., 1994). Besides providing disease resistance to the plants, SA can modulate plant responses to a wide range of oxidative stresses (Shirasu et al., 1997). It plays an essential role in preventing oxidative damage in plants by detoxifying superoxide radicals (Bowler et al., 1992) and by altering antioxidant capacity and antioxidant enzyme activities in plants (Chen et al., 1997; Dat et al., 1998, Fodor et al., 1997; Larkindale & Huang, 2004; Mohammed & Tarpley, 2009b; Rao et al., 1997; Wang & Li, 2006). Plants pre-treated with SA have shown increased thermotolerance (Larkindale & Knight, 2002).

3.1 Effects of plant growth regulators on plant morphology and physiology under high night temperature

Exogenous application of PGRs on plants under high night temperatures have shown positive, negative or no effect on plant morphology. Exogenous foliar application of GB or SA did not affect plant height in rice (Fig. 4). However, Farooq et al., (2008a, 2008b) state that seed priming of maize (*Zea mays* L.) with GB or SA increased shoot length, root length and biomass production. Increase in plant height as a result of SA application is due to increased cell enlargement, endoreduplication and/or cell division (Kang et al., 2007; Vanacker et al., 2007).

Glycine betaine and SA have profound effects on crop production through their effects on crop physiology. Foliar application of GB or SA increases leaf photosynthetic rates and decreases internal CO_2 concentration, respiration rates and membrane injury in rice (Fig. 5). Similar results were seen in other crop species and growth conditions where application of GB or SA increased photosynthetic rates and decreased respiration rates and injury to the membranes (Farooq et al., 2008a; Khan et al., 2010; Zhou et al., 1999).

In rice, application of GB or SA did not affect leaf chlorophyll or nitrogen content (Fig. 5). However, studies have shown that exogenous application of GB stabilizes pigments and prevents water oxidation and photooxidation (Cha-um et al., 2006, Sakamoto et al. 1998). Stabilization of pigments (chlorophyll and carotenoids) aids in light energy capture as required for photosynthesis. Several studies have reported that application of GB aids in

protecting the photosynthetic machinery of the plant organelles by stabilizing the ultrastructure of the chloroplast, photosystem-II reaction centers and maintaining the oxygen-evolving machineries (Allakhverdiev et al., 2003; Busheva & Apostolova, 1997; Lee et al., 1997; Makela et al., 2000; Pospisil & Dau 2000; Sakamoto & Murata, 2000). On the other hand SA increases photosynthetic efficiency by increasing pigment concentrations and protecting photosystem function via activation of antioxidant defense systems as a signaling molecule (Dat et al., 1998; Ervin et al., 2005; Senaratna et al., 2001). The other physiological parameters such as respiration rates, transpiration rate and injury to leaf membrane decreased with application of GB or SA (Mohammed & Tarpley, 2011b). Studies have reported antitranspiration effects of GB and SA applications in crop species suggesting that GB and SA play an important role in controlling stomatal opening and closing under stress conditions (Cha-um et al., 2006; Khan et al., 2010; Larque-Saavedra, 1978). The most important effect of PGR's on crop production is through their ability to maintain the integrity of the membranes. The functional cell-membrane system is central to crop productivity. Stable membranes facilitate free movement of ions and water across the membrane and provide a favorable environment for enzymes and thylakoid membrane activities (Björkman et al., 1980). Several studies have reported that GB or SA application can maintain membrane integrity under stress conditions (Bohnert & Jensen, 1996; Farooq et al., 2008a, 2008b; Hussain et al., 2008; Mohammed & Tarpley, 2011b; Pan et al., 2006) by up regulating antioxidant enzyme activities and total antioxidant capacity (Demiral & Türkan, 2004; Farooq et al., 2008a, 2008b; He et al., 2005; Mohammed & Tarpley, 2009b).

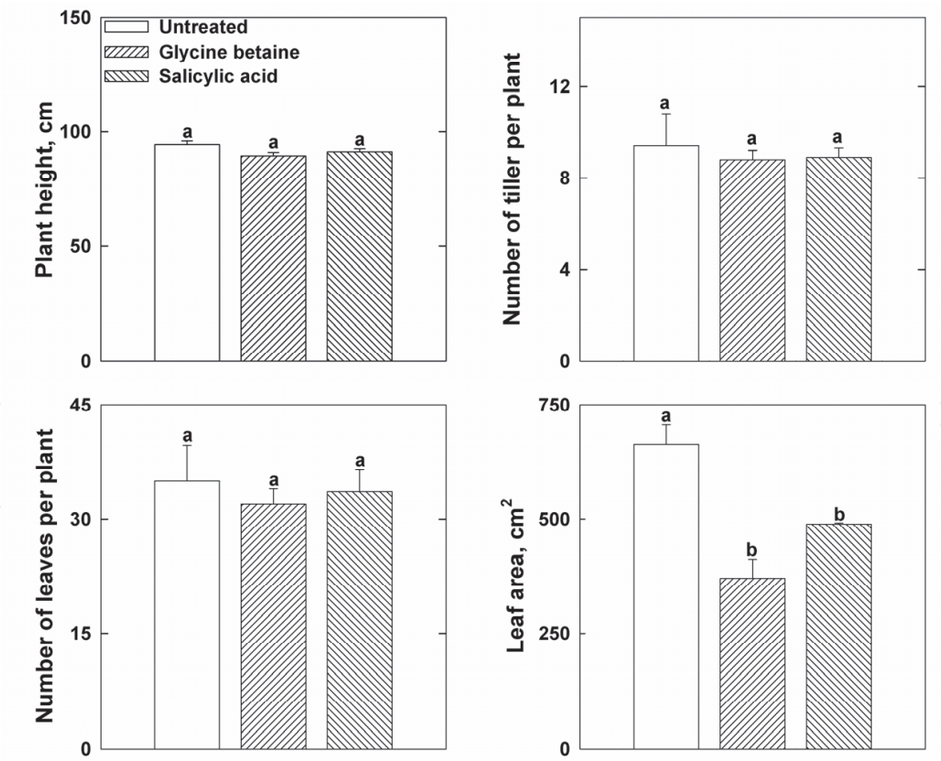


Fig. 4. Effects of glycine betaine and salicylic acid on rice morphology under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

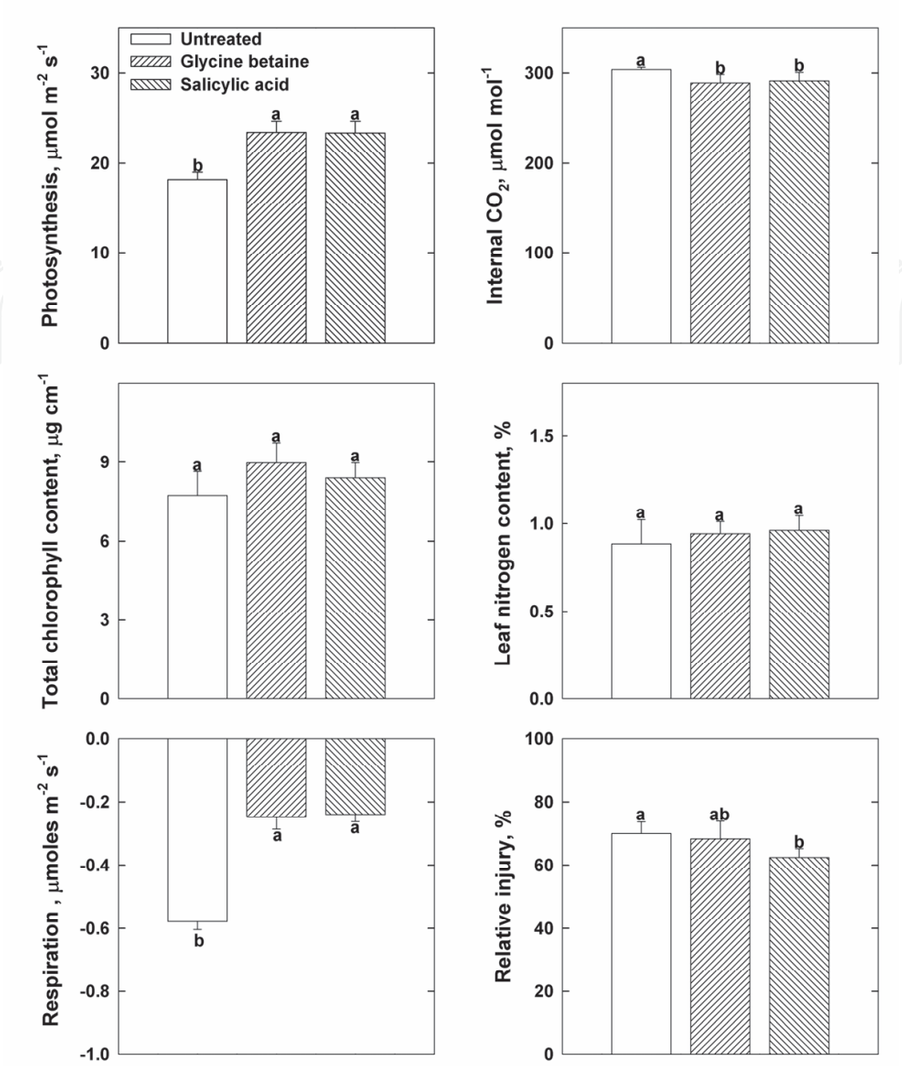


Fig. 5. Effects of glycine betaine and salicylic acid on rice physiology under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the P<0.05 level.

3.2 Effects of plant growth regulators on plant antioxidant enzyme activities and total antioxidant capacity under high night temperature

The antioxidant status of the plant is closely associated with its stress tolerance (Smirnoff, 1995). The severity of ROS-induced damage depends upon the antioxidant status of the plant and activities of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (AP), catalase (CAT) and glutathione redutase (GR). Many studies have shown an increase in endogenous antioxidant levels as a result of exogenous application of GB or SA (Chen et. al., 1997; Diaz-Zorita et. al., 2001; Fang et al., 2009; Mohammed & Tarpley, 2009b). In rice, exogenous application of GB or SA increased total antioxidant capacity under high night temperature (Fig. 6). These increases in the levels of endogenous antioxidant are due to increases in antioxidant enzyme activities (Demiral & Türkan, 2004; Farooq et al., 2008a, 2008b; He et al., 2005; Khan et al., 2010).

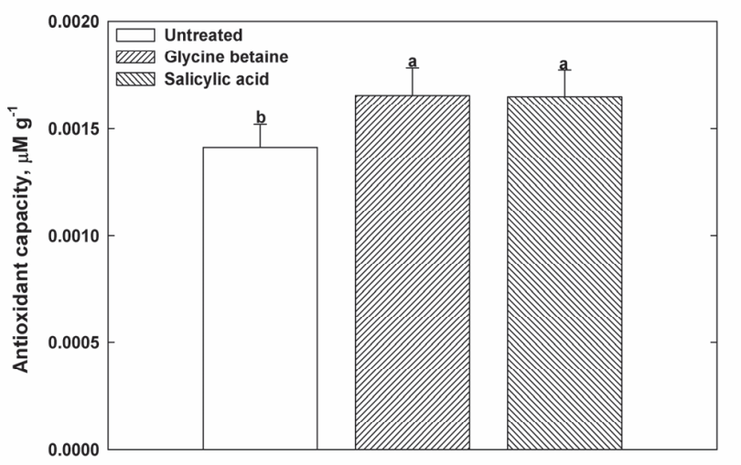


Fig. 6. Effects of glycine betaine and salicylic acid on total antioxidant capacity under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

3.3 Effects of plant growth regulators on yield and yield-related parameters under high night temperature

Rice phenology under high night temperature was not altered by exogenous application of GB or SA as indicated by 1st panicle emergence date (Fig. 7). However, previous studies by Oota (1975) and Datta & Nanda (1985) showed that SA application induces early flowering in duckweeds (*Lemna gibba* L.) and chenna millet (*Panicum miliaceum* L.). Exogenous application of GB or SA increased spikelet fertility in rice (Fig. 7). The increase in spikelet fertility was due to increased photosynthesis, and decreased respiration and injury to the membrane stability as a result of GB or SA application. Exogenous application of GB or SA increases stability of the membranes as a result of increased antioxidant capacity of the plants. The enhanced membrane stability is responsible for increased photosynthesis and decreased respiration, which in turn increases crop production. In a nutshell, exogenous applications of GB or SA have been shown to increase stress tolerance, and often enhance plant growth and final crop yield under stress conditions, including HNT.

4. Conclusion

Yield, the final manifestation of all the physiological processes, decreased due to high night temperatures. The decrease in crop yields as a result of HNT was due to increased respiration and decreased photosynthesis and membrane stability. The decrease in photosynthesis was associated with decreases in photosynthesis-governing parameters such as stomatal conductance, internal CO_2 concentration, leaf chlorophyll content and leaf nitrogen, as a result of HNT. Moreover, decreased crop growth duration, pollen production and viability also contributed to decreased yields under HNT. Exogenous application of PGRs such as GB and SA increased production of photosynthates and decreased consumption of photosynthates and injury to the membrane, thereby increasing crop productivity under HNT. The exogenous application of GB and SA increases antioxidant levels, thereby protecting the membranes and enzymes against heat-induced ROS-mediated degradation, thus increasing crop productivity. However, there is a significant variation in

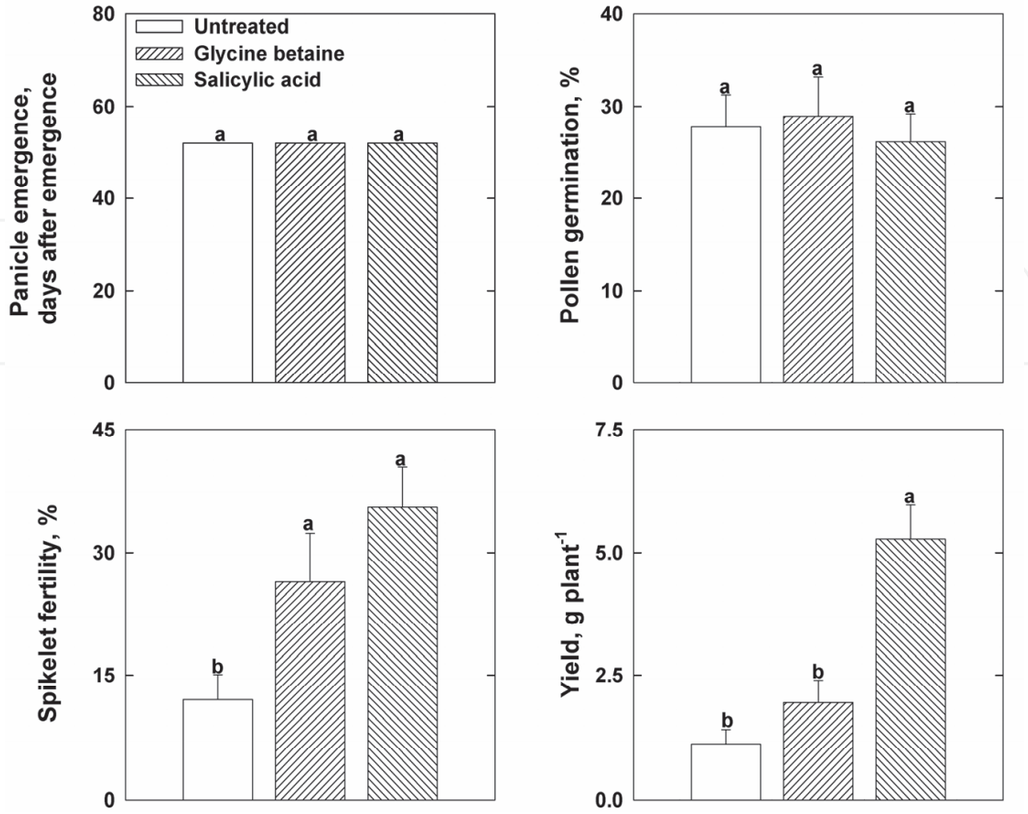


Fig. 7. Effects of glycine betaine and salicylic acid on rice yield-related parameters under high night temperature. Each bar represents average ± S.E. Different letters indicate means are significantly different at the $P<0.05$ level.

response to exogenous application of PGRs such as GB and SA among different plant species. This varied response among the plant species is due to 1) plant quantitative response to exogenous application of PGRs such as GB and SA at different stages of plant development, 2) plant exhibition of different responses to PGRs such as GB and SA at different stages of plant development and 3) variation in the effective concentration of a particular PGR among species. The PGRs such as GB and SA provide an option to protect the plants from different stresses like high day temperatures, high night temperature, drought and salinity, however, over-application of the PGRs such as GB and SA may be toxic to some plants resulting in growth inhibition or yield reduction.

5. Acknowledgment

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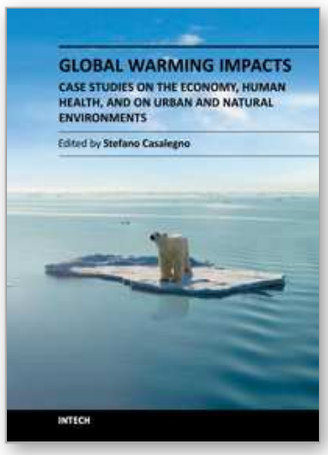
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This book addresses the theme of the impacts of global warming on different specific fields, ranging from the regional and global economy, to agriculture, human health, urban areas, land vegetation, marine areas and mangroves. Despite the volume of scientific work that has been undertaken in relation to each of each of these issues, the study of the impacts of global warming upon them is a relatively recent and unexplored topic. The chapters of this book offer a broad overview of potential applications of global warming science. As this science continues to evolve, confirm and reject study hypotheses, it is hoped that this book will stimulate further developments in relation to the impacts of changes in the global climate.

How to reference

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