

The Current Situation in the US Rice Industry and the Results from Night Temperature Effects

Lee Tarpley and Abdul R. Mohammed
Texas AgriLife Research, Texas A&M University System
1509 Aggie Drive, Beaumont, Texas, U.S.A.
ltarpley@tamu.edu

Abstract: The rice-growing region in the southern U.S. with its hot and humid summer is susceptible to rice crop yield loss due to an increased frequency of periods with high night temperatures. Given the occurrence of such periods of high temperatures being implicated in rice yield losses in some recent years, a combination of altered crop management strategies and crop genetic improvement is needed to minimize both current and intermediate-term effects of global warming on southern U.S. rice production. Research in the U.S. concerning the effects of high temperatures on crops has been strongly influenced in direction by research conducted using Soil-Plant-Atmosphere-Research chambers. These studies have traditionally examined interactions among global climate change variables. With respect to the effect of high temperatures on diverse agronomic crops, decreased pollen production, pollen germination and spikelet fertility, as well as decreased membrane stability, have been generally implicated as affecting crop yield. Southern U.S. rice milling quality is decreased by high temperatures, especially high night temperatures, and appears to be associated with an increase in chalkiness. The primary effects of high night temperature on southern U.S. rice yield appear not to be due to decreased production of photosynthates or through altered rice morphology, but rather are through increased consumption of photosynthates, accelerated rate of plant development, and decreased reproduction. The high night temperatures appear to be partially acting through heat induced reactive-oxygen-species-mediated degradation of membranes and enzymes (i.e., oxidative stress).

Keywords: rice, crop production, heat stress, United States, high night temperature

1. Introduction

This report describes recent (published 2005 or later) research conducted in the United States (U.S.) concerning heat stress effects on crop production. While some mention is made of the effects of high temperatures on aspects of wheat crop productivity, the emphasis shall be on rice crop productivity. The major portion of the report on rice will consist of the effects of high night temperatures on southern U.S. rice growth, development and physiology.

The U.S. rice production occurs in two areas, California and the southern U.S. In California, the relative humidity is low (less than 70% RH typically, often much lower [1], so the occurrence of high night temperatures drastically affecting rice production is unlikely (average daily low temperatures do not exceed 19°C [1]). In contrast, much of the southern U.S. rice production area (consisting of the states of Arkansas, Missouri, Mississippi, Louisiana and Texas) (Fig. 1) has hot and humid summers, with average daily maximums and minimums exceeding 32°C and 21°C, respectively, from June through August [1], the time of the year that includes the rice reproductive period. A practical concern expressed by rice farmers of the southern U.S. regarding global warming is the potential for an increased incidence of days during the rice growing season with temperatures hot enough to hurt yield through direct effects on rice crop growth, development or physiology. Given the occurrence of such periods of high temperatures being implicated in rice yield losses in some recent years, a combination of altered crop management strategies and crop genetic improvement is needed to minimize both current and intermediate-term effects of global warming on southern U.S. rice production.

Heat stress effects on cereal crops can be summarized as effects on growth, development or physiology. In addition, for food grains, the effects on grain quality have been examined in several studies, but are only briefly mentioned here.

2. Recent U.S. Research Concerning Heat Stress Effects on Crops

1) Recent U.S. Research Concerning Heat Stress Effects on Cereal Crops Other Than Rice or Wheat

Researchers in the U.S. have studied heat stress effects on a number of crops and through diverse approaches. Several of the groups providing a detailed response of plants to high temperatures use arrays of SPAR chambers (Soil-Plant-Atmosphere-Research chambers) [2], which are large sunlit chambers with controlled temperature and atmospheric composition (Fig. 2). The construction provides the advantage of applying complex regimes of temperature and, to a lesser extent, atmospheric composition. In addition, canopy (albeit small canopy) measurements of photosynthesis, respiration and water use can be obtained. Because an array (e.g., 5 to 15) of chambers depending on the study site are used, interactions among environmental factors (e.g., air temperature and nutrient fertility) can be examined. On the other hand, the limited number and size of the chambers, and their emphasis on providing canopy-level measurements, limit the number of factors or replications that can be examined simultaneously, as well as the intensity of periodic destructive sampling. Three of the groups utilizing SPAR

chambers have focused on agronomic crops. These locations are Starkville, Mississippi (K.R. Reddy); Beltsville, Maryland (V.R. Reddy); and Gainesville, Florida (K. Boote and H. Allen). The Gainesville group conducted a number of studies on rice as affected by high temperatures and elevated CO₂; the Beltsville group has conducted a study or two with rice. Example recent studies from these groups on crops other than rice directly follow.



Fig. 1. Location of the U.S. rice-growing regions. California (CA) to the west and the Southern (or Mid-South) region containing parts of Arkansas (AR), Louisiana (LA), Mississippi (MS), Missouri (MO) and Texas (TX).

At Gainesville, Vara Prasad, Boote and Allen [3] examined grain sorghum exposed to particular temperature regimes (32/22, 36/26, 40/30, and 44/34 °C (day maximum/night minimum) at ambient (350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) or elevated (700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) from emergence to maturity. The lower seed-set at high temperatures in this study was due to lower pollen production and lower pollen germination, however, the role of stigma receptivity was not eliminated. Elevated CO₂ increased foliage and seed temperatures, which extended the negative effects of the higher chamber temperatures on the grain-sorghum productivity.

At Beltsville, Kim and colleagues [4] also examined the interaction between growth temperature (19/13 to 38.5/32.5 °C (day maximum/night minimum) and atmospheric CO₂ levels (ambient [370 $\mu\text{mol CO}_2 \text{ mol}^{-1}$] and doubled [750 $\mu\text{mol CO}_2 \text{ mol}^{-1}$]) upon vegetative development and photosynthesis of maize. Although the growth, photosynthesis and development of the maize plants were affected by temperature with the optima for leaf photosynthetic capacity and for leaf appearance rate near 34 and 31 °C, respectively; the atmospheric CO₂ concentration had little effect, either independently or in interaction with temperature, on these processes.

At Starkville, Koti et al. [5], examined the interactive effect of temperature (30/22 and 38/30 °C), atmospheric CO₂ level (360 and 720 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) and UV-B radiation intensity (0 and 10 $\text{kJ m}^{-2} \text{ d}^{-1}$) on vegetative development of six soybean genotypes (grown in pots inside the SPAR chambers) representing five maturity groups. The interactive effects on reproductive development of these genotypes have been previously reported [6]. The elevated temperatures and elevated UV-B radiation levels tended to cause more injury (e.g., decreased membrane stability) to the soybean genotypes, while elevated CO₂ usually partially compensated for this. The rank genotype response was, however, altered by the interactive effects of the three climate change factors. For example, in some genotypes, the presence of the elevated CO₂ increased the injury levels. In reproduction, the UV-B and/or elevated temperature led to smaller flowers, less pollen per flower and decreased pollen germination. Elevated CO₂ did not provide any compensatory benefit. The genotypes that were classified as tolerant based on reproductive measurements were not the same as those considered tolerant based on vegetative development measures.

The Mississippi group also examined in vitro pollen germination, pollen tube length, and relatively injury (membrane stability) under various temperatures for pollen collected from field-grown cotton cultivars, and developed a procedure for classifying cultivars as tolerant or susceptible based on this information [7].

A moderate number of other (not using SPAR chambers) studies have been conducted concerning the effects of high temperatures on various crops besides rice or wheat. These have progressively included an interest in the night temperatures as part of the study. For example, Albertine and Manning [8] examined the interaction of elevated night soil temperatures and elevated ozone on germination and early growth of bean, concluding that while the elevated night temperature increased germination and seedling growth rate, it also increased susceptibility to ozone damage, with the onset of ozone damage occurring earlier in plants subjected to the elevated night soil temperatures.



Fig. 2. The Soil-Plant-Atmosphere-Research (SPAR) chambers at Starkville, Mississippi, USA. The SPAR facilities in Florida, Maryland, and Mississippi have been influential in US research concerning the effects of high temperatures and other climate change factors on crop production.

2) Recent U.S. Research Concerning Heat Stress Effects on Wheat

Several recent U.S. studies have examined the effect of high temperatures on wheat grain quality. These studies are not included in this report.

Tewold et al. [9] evaluated a number of common Texas wheat cultivars for tolerance to high post-heading temperatures. The high temperatures were allowed to be provided naturally due to the planting location at Uvalde in southwest Texas and also due to a delayed planting in one of the two seasons. Evaluated across genotypes, yield was negatively correlated with the daily mean temperature (obtained from a weather station at the experimental farm) averaged over the post-heading period of the individual cultivars. This was especially true in the hotter season. There was a wide range of yield variation among cultivars. Those that were highest yielding under these hot post-heading environments were those that were early heading. These cultivars had a longer duration of the post-heading period, thus a longer grain-filling period; these cultivars also completed more of their grain filling while temperatures were lower. The earlier-heading cultivars also had a greater proportion of green leaves remaining at anthesis. Although these earlier-heading cultivars produced fewer total leaves per tiller, they lost fewer leaves to senescence at anthesis than the later-heading cultivars.

Ristic et al. [10], a group at Kansas State University, established the use of chlorophyll content as a surrogate for chlorophyll fluorescence as a screening tool for heat tolerance in winter wheat cultivars. Greenhouse-grown potted plants were moved to an environmental chamber near the beginning of flowering for a 16-day high temperature exposure (36/30 °C (day/night)). Chlorophyll content (determined with a chlorophyll meter) was strongly negatively associated with the chlorophyll fluorescence, and both showed consistent cultivar patterns for variation with duration of exposure to the heat stress.

In Prasad et al. [11], the Kansas State group studied the effects of high night temperatures, using two wheat cultivars grown in environmental chambers in which the night temperature was varied (either 14, 17, 20 or 23 °C) starting at boot stage, where a 24/14 °C (day/night) regime was considered optimal. Many of their findings are in line with current understanding of plant response to heat stress. For example, the high night temperatures decreased photosynthesis, grain yields decreased with increasing night temperature; and spikelet fertility, grains per spike, and grain size were decreased. In addition, grain filling duration was decreased under the higher night temperatures.

Hays et al. [12] at Texas A&M University examined the effect of a one-day high day temperature at 10 days after pollination on wheat kernel abortion and weight of a susceptible and tolerant variety. The heat exposure decreased the percentage of filled kernels and decreased the kernel weight in the susceptible variety, but not the tolerant one. Application of 1-methylcyclopropane, an ethylene receptor inhibitor, blocked the higher ethylene production observed in the susceptible variety upon exposure to the high temperature, and also prevented the reduction in filled kernel percentage and in kernel weight, thus suggesting that the high temperature caused its effect through a stimulation of ethylene synthesis in the susceptible variety.

3) Recent U.S. Research Concerning Heat Stress Effects on Rice

In 2004, Baker [13] reported on the response of several southern U.S. rice cultivars to various temperatures and elevated atmospheric CO₂. These studies were conducted in various ways over several years using the SPAR facilities at Beltsville. The primary effect of temperature was upon the number of grains per panicle, not on the

number of panicles. Baker also tentatively concluded that the southern U.S. cultivars might be more sensitive to high temperatures than the Asiatic (*indica* or *japonica*) cultivars. The southern U.S. rice cultivars appeared to have a day temperature limit of 32 to 35 °C, albeit this was at elevated CO₂, thus might have been impacted by an elevated tissue temperature.

The SPAR facility at Gainesville, Florida was used to conduct a number of studies of rice response to temperature and elevated CO₂, with most of these being conducted in the 1990s. However, a fairly recent study by the Gainesville group is presented in Prasad et al. [14], which concerned a study conducted in temperature-gradient houses, rather than in the SPAR chambers. The study thus was focused on high-temperature stress only (ambient [28/22 °C day/night] vs. ambient + 5°C, both day and night). A number of rice varieties representing different species, ecotypes and origins were screened. Spikelet fertility was evaluated, as were phenology, pollen number and viability, leaf photosynthesis, leaf membrane thermal stability, and time-of-day of anthesis. The elevated temperature did not have a consistent effect on development rate or on vegetative biomass, but did decrease grain yield. The relatively low decrease in yield due to the elevated temperature that was observed in IR-72 and IR-8 was partially explained by an avoidance of the high temperatures due to late flowering relative to the other varieties. The N-22, a tropical *indica* variety from India had the last decline in yield due to elevated temperature, and also the least decrease in spikelet fertility, thus was considered relatively tolerant to high temperatures. Among varieties, the effects on pollen production and pollen reception (number of pollen grains on the stigma surface) were similar as those on spikelet fertility. The elevated temperature decreased pollen viability (I-KI staining of starch in pollen indicating potential viability) across varieties. The photosynthetic rate of the flag leaf measured at anthesis for plants exposed to the elevated temperatures was lower on average compared to those subjected to ambient temperature, but differences among cultivars were not consistent with yield decreases. The relative injury (calculated from the leaf membrane thermal stability) due to the elevated temperatures was fairly consistent among varieties ranging from 44.1 to 55.6%. Among the *O. sativa* varieties, those with the longest duration from emergence to heading also tended to have an earlier “latest time-of-day of anthesis.” Lower grain yield due to the elevated temperature and the differential response of the varieties to the elevated temperature were associated with lower spikelet fertility, which was primarily associated with decreased pollen production and pollen shed.

Starting in 2005, a group from the University of Arkansas published several articles focusing on the effects of high temperatures, particularly high night temperatures, on rice grain quality (Counce et al. [15]; Cooper et al. [16]; Cooper et al. [17]). The 2005 article [15] presents research concerning the effect of high night temperatures (18 vs. 24°C imposed in a growth chamber from 0000 h to 0500 h starting at 50% heading). The cultivars used, Cypress and LaGrue, were popular in the late 1990s and early 2000s, with Cypress being well-known for an excellent milling quality. The higher night temperatures resulted in reduced head rice yields and grain width for each cultivar. Cooper et al. (2008) [17] moved plants into phytotrons at night temperatures of 18, 22, 26 or 30°C starting at the late anthesis/grain filling initiation stage. Increasing night temperatures generally decreased head rice yield and grain dimensions. The number of chalky kernels generally increased with an increase in night temperature, and it was this increase in chalkiness that seemed most closely related to the decrease in head rice yield. In Cooper et al. (2006) [16], the same group evaluated rice milling quality variation, especially head rice yield, in a 17-year historical dataset for two long-grain cultivars (Newbonnet and Lemont), which included head rice yield and days to 50% heading, in relation to historical weather data. The authors estimated growth staging data using degree day information. The single variable that contributed most (25% of the variance) to explaining the head rice yield was night temperature during the period soon after the first kernel of the main panicle had matured, with the night temperature negatively associated with decreased head rice yields.

4) Recent Research at Beaumont, Texas, U.S.A. Concerning Effects of High Night Temperature on Rice Growth, Development and Physiology

Mohammed and Tarpley, located at the Texas AgriLife Research and Extension Center at Beaumont, have recently conducted several studies [18, 19, 20] detailing the response of southern US rice cultivars to elevated night temperature. The rice-growing area along the US coast of the Gulf of Mexico, which includes parts of Louisiana and Texas, is susceptible to an increased frequency of periods of heat stress, especially those of high night temperatures (e.g., in 2006 at Beaumont, the average night temperatures varied between 26 and 28°C during the rice crop reproductive period). The principal cultivar investigated that was Cocodrie, which has been one of the most popular cultivar grown in Texas and Louisiana over the last seven or eight years.

Mohammed and Tarpley devised an apparatus to allow carefully controlled heating of small populations of plants in the absence of enclosures [18]. The apparatus (Fig. 3) can be used to apply elevated heat treatments to plant canopies in the open field or in the greenhouse, and can accept either square-wave application of elevated temperature or a complex prescribed diurnal or seasonal temperature regime. The heating system of the present study uses overhead infrared heaters which are relatively inexpensive and are accurate and precise in rapidly controlling the temperature. The apparatus successfully maintained air temperatures within the set points ± 0.5 °C.

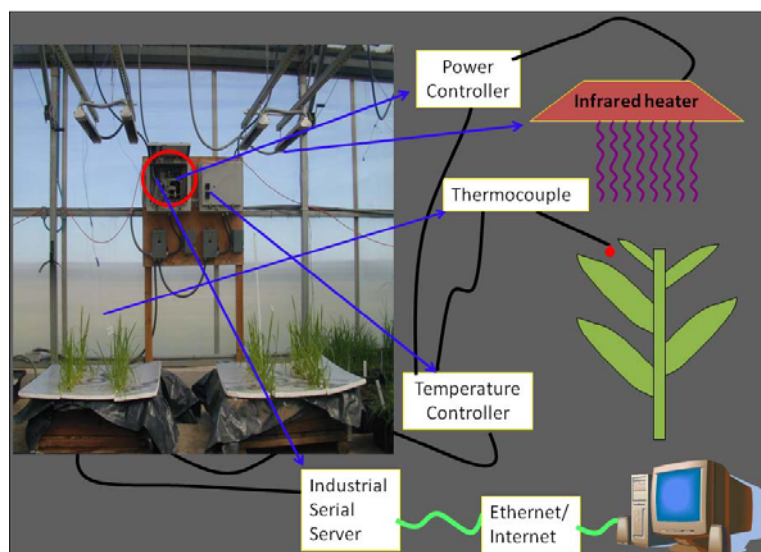


Fig. 3. Graphic illustrating the infrared heating apparatus used for high night temperature studies at Beaumont, Texas, USA. The apparatus provides controlled prescribed heating of small populations of plants in the absence of an enclosure. Figure from Mohammed and Tarpley [18].

In a series of experiments [19, 20], Mohammed and Tarpley compared elevated night (2000 to 0600 h) temperatures (32°C) to ambient (27°C), with exposure starting 20 days after emergence and continuing until grain maturity. The respiration rates, membrane thermo-stability, total antioxidant capacities of leaves, leaf photosynthetic rates, leaf chlorophyll concentration, leaf nitrogen concentration, percent pollen germination, spikelet fertility, morphology, phenology, and grain characteristics were investigated. In addition to the temperature treatments, the plants were treated with exogenous plant growth regulator treatments. These included α -tocopherol (vitamin E), glycine betaine (GB) and salicylic acid (SA), which play important, but different, roles in inducing thermo-tolerance in many plant species.

The high night temperatures did not affect rice morphology or rice leaf photosynthetic rates, however, the high night temperatures decreased pollen germination (20% less) and spikelet fertility (72% less) (Fig. 4).

In addition, the high night temperatures increased leaf respiration rates (21% more), and decreased membrane thermo-stability (60% less) [20], grain length (2% less), and grain width (2% less). The high night temperatures also sped up the rice plant development rates, as indicated by the panicle emergence date. The combination of these effects decreased the rice yield by 90%. Although the high night temperatures decreased leaf chlorophyll concentration (7%) and leaf nitrogen concentration (18%), these were not associated with leaf photosynthetic rates. Application of glycine betaine or salicylic acid increased the total antioxidant capacity of the rice plants by 17% [20], thereby decreasing leaf respiration rates, and increasing membrane thermal stability, pollen germination, and spikelet fertility, thus increasing the yield.

Glycine betaine and salicylic acid increased yield of Cocodrie rice plants under ambient night temperature (27°C), as well as under high night temperature (32°C), suggesting that either 27°C is a superoptimal night temperature for Cocodrie, a popular southern US rice cultivar, or that factors in addition to high night temperature were contributing to oxidative stress in these studies.

3. Conclusions

The primary effects of high night temperature on rice productivity appear not to include decreased production of photosynthates or altered rice morphology, but rather are increased consumption of photosynthates, accelerated rate of plant development, and decreased reproduction. The high night temperatures appear to be partially acting through heat induced reactive-oxygen-species-mediated degradation of membranes and enzymes (i.e., oxidative stress).

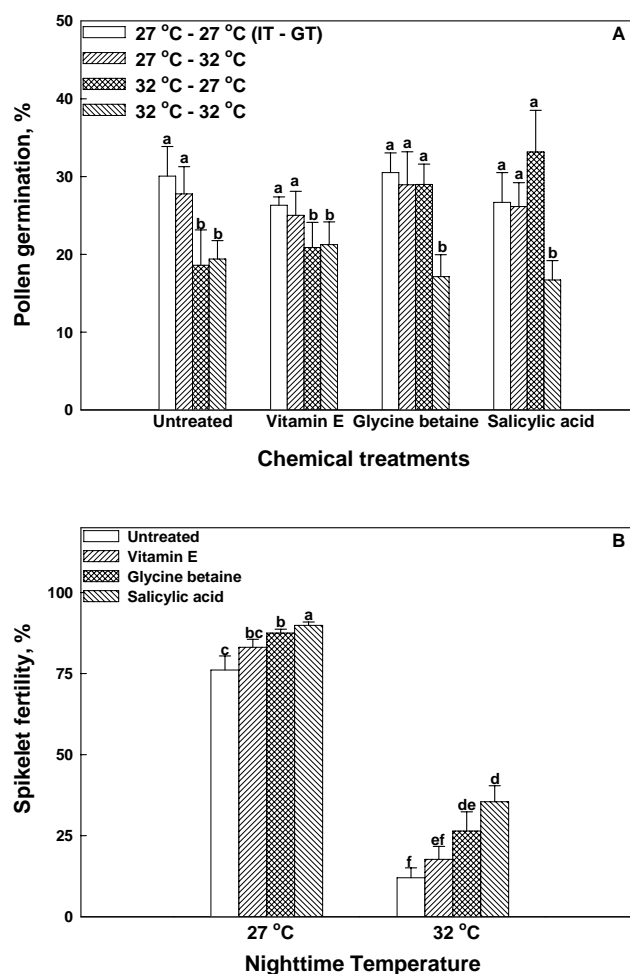


Fig. 4. Effects of night temperature and plant growth regulators on pollen germination (Panel A) and spikelet fertility (panel B). For pollen germination, all values are mean \pm standard error, $n = 10$; for spikelet fertility, all values are means \pm standard error, $n = 13$. Different letters indicate means are significantly different at the $P < 0.05$ level. Figure from Mohammed and Tarpley [19].

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