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Elevated Temperature and CO_2 Impacts on Pollination, Reproductive Growth, and Yield of Several Globally Important Crops

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Abstract

Experiments were conducted to determine effects of elevated temperature and doubled carbon dioxide (CO_2) on pollination, reproductive growth, and yield of rice, soybean, peanut, and dry bean. Diurnal temperature treatments were 28/18, 32/32, 36/26, 40/30, and 44/34°C, at 350 or 700 μmol CO_2 mol^{-1}. Vegetative growth was tolerant of high temperature; however, reproductive growth failed at stressfully high temperatures. Above 25°C, rice grain yield and harvest index (HI) declined progressively, reaching zero at 36°C mean temperature, associated with decline in filled grain percentage attributed to failed pollination. Dry bean was more sensitive, with highest yield and seed size at 23°C, reaching zero at 32°C. Soybean and peanut were more tolerant than rice; their grain yield and HI declined as temperature exceeded 26°C, reaching zero at 40°C. Pollen viability of bean and peanut followed a temperature response similar to grain yield and was a major factor in yield decline, although seed size also decreased. Rice maintained grain-size with rising temperature whereas soybean, peanut, and bean seed size declined at elevated temperatures. While elevated CO_2 increased grain yield, there were no beneficial interactions of CO_2 with elevated temperature. Detrimental effects of elevated temperature on reproductive processes will be very important under future global change.

Keywords: Carbon dioxide, Elevated temperature, Pollination, Seed-set, Seed yieldIntroduction

1. Introduction

Global climate change is anticipated as a result of continuing increase in atmospheric carbon dioxide (CO_2) and other greenhouse gases. The atmospheric CO_2 is projected to increase from present day values of 370 μmol mol^{-1} up to 540 to 970 μmol mol^{-1} by the year 2100, depending on fossil fuel emissions and other factors (Prentice *et al.*, 2001). With this increase in greenhouse gases, a rise in global mean temperature in the range of 1.4 to 5.8 (3.6 mean) °C is predicted by atmospheric general circulation models (Cubasch *et al.*, 2001). Such increases in global mean temperature are expected to have adverse impacts on reproductive processes and grain yield of important seed-producing crops in many regions of the world. Thus, it is important to understand mechanisms by which elevated temperature may limit reproductive processes of seed-producing plants. While many research studies have shown that increased CO_2 enhances productivity of grain crops by 30 to 35% (Kimball, 1983; Ainsworth *et al.*, 2002; Kimball *et al.*, 2002), there have been fewer studies on effects of elevated temperature on grain crops and the effects to-date appear to be detrimental. Thus, the objective of this paper is to report results of our research on the effects of elevated temperature in combination with CO_2 on several important grain crops, with emphasis on reproductive processes that may fail or be adversely affected at elevated temperature. Our findings will be compared to literature reports of other studies.

2. Materials and Methods

These studies were conducted in eight sunlit, controlled-environment chambers at the University of Florida developed specifically for investigating effects of global climate change factors on plants. Each chamber measures 2 m by 1 m land area, with 1.5 m height, with clear polyethylene telephtalate "SIXLIGHT" plastic film on an aluminum frame, placed over an insulated soil lysimeter that is 0.6 m deep. Engineering descriptions of the control systems of these plant growth chambers can be found in Jones *et al.* (1984) and Pickering *et al.* (1994). Recent descriptions of the use of the system for plant growth studies are available in Allen *et al.* (2003) and Prasad *et al.* (2003). Plants were grown from sowing to maturity as a closed stand under natural sunlight cycle and intensity of the Gainesville location (29° 40'N). Air temperature was programmed to follow a natural diurnal cycle described by maximum/minimum temperature set-points. Typical temperature treatments were 28/18, 32/22, 36/26, 40/30, and 44/34°C, following a sinusoidal shape during the day and a decay function at night, as suggested by Parton and Logan (1981). The difference between day/night maximum/minimum was 10°C, to mimic a humid climate. Temperature levels were controlled to within

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± 0.2 °C of set-point. Dewpoint temperatures were controlled such that relative humidity for each treatment was 40-42% at 1500 h. The daytime CO_2 levels were controlled to either 350 or 700 μmol mol^{-1}, with accuracy of ± 1.0 μmol mol^{-1}, using mass flow controllers, as described by Allen *et al.* (2003). In the first five rice experiments, the temperatures followed a square wave, constant day/constant night temperature, and the daytime CO_2 levels were controlled to either 330 or 660 μmol mol^{-1}. On a 5-min interval, canopy carbon exchange rate was determined from mass flow meter injection of CO_2 to maintain constant CO_2, and canopy evapotranspiration was measured as water collected from cooling coils into a tipping bucket rain gauge. The soil type was a Kendrick fine sand topsoil (loamy siliceous hyperthermic Arenic Pauleudult) that was 0.55-m deep.

During the past 15 years, we grew rice (*Oryza sativa* L.), soybean (*Glycine max* L. Merr.), dry bean (*Phaseolus vulgaris* L.), and peanut (*Arachis hypogaea* L.) from sowing to maturity in these chambers under treatments that include a wide range of temperatures and CO_2 levels. The rice was sown direct-seeded in 0.18-m rows and thinned to 235 plants m^{-2}. Flood water of 50 mm depth was applied at the second leaf stage of rice and maintained until maturity. Paddy water temperature was controlled in the first five studies at the mean daily treatment temperature. Rice cultivars included IR30, M103, and IR72. Soybean cv 'Bragg' MG 7 was sown and thinned to 75 plants m^{-2} in 0.33-m row spacing. A Red Kidney type of dry bean cv 'Montcalm' was sown and thinned to 27 plants m^{-2} in 0.33-m row spacing. Peanut cv 'Georgia Green' was sown and thinned to 20 plants m^{-2} in a twin-row spacing arrangement (two rows 0.24-m apart, but on 1.0-m row centers). Grain legumes were surface-irrigated for the first 20 days, and then subirrigated by an automated float system that maintained a constant water table at 0.45-m soil depth. Rice was well-fertilized with 8.4 g N m^{-2} prior to sowing, plus three split applications of 4.2 g N m^{-2} every 3 weeks. All crops were adequately fertilized with P and K. Black woven polypropylene fiber shades were maintained at canopy height along the outside of the chambers to mimic a light environment similar to that of border rows in a field crop. Some studies included measurements of pollen viability, seed-set percentage, single-seed growth rate, seed filling period, leaf photosynthesis, and the percentage of filled grains at maturity. All studies included measurements of final biomass, grain yield, seed harvest index, and seed size. Determination of final biomass and grain yields were usually derived from the entire 1 x 2 m land area sample at maturity, depending on species.

3. Results and Discussion

We conducted a total of six experiments on rice. The first five were conducted on the IR30 cultivar and were previously summarized (Baker and Allen, 1993a, 1993b; Baker *et al.*, 1992, 1995, 1996). These experiments illustrated good repeatability of the effects of elevated temperature and CO_2 levels. The first important conclusion is that vegetative growth and total biomass were not affected as much by elevated temperature as was rice grain yield (Fig. 1a).

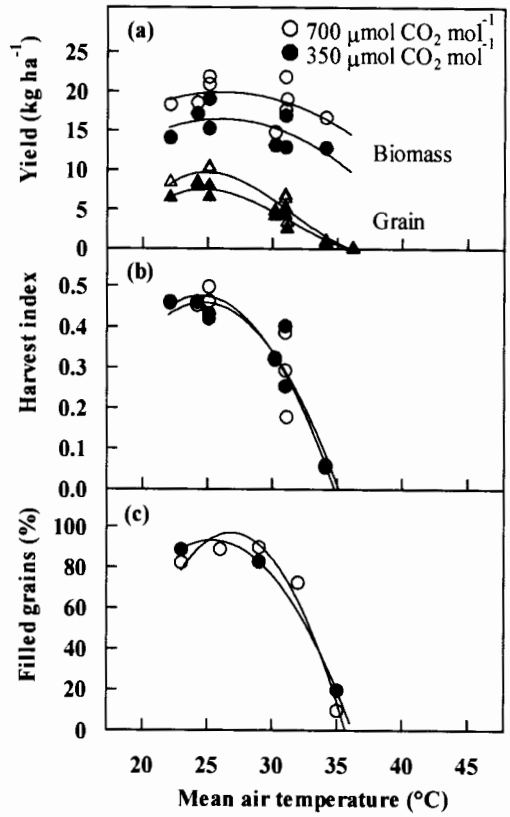

Fig. 1. (a) Biomass and grain yield of rice cv. IR30, (b) harvest index of cv. IR30, and (c) percent filled grains of cv. M103, in response to air temperature and [CO_2]. Results of five studies on IR30 (Baker et al., 1995) and one on M103 (Snyder, 2000).

The optimum daily mean temperature for rice grain yield and harvest index (HI) was 25 °C, and yield declined 10% for every degree °C temperature increase from 26 to 36°C (Baker *et al.*, 1993a). At mean temperature of 36°C, grain yield was zero because of failure to produce filled grains (we attributed this to pollen sterility). The result of this reproductive failure, was that grain harvest index (Fig. 1b) was optimum at 25°C and curvilinearly reached zero at 36°C mean temperature. Figure 1a was first reported in the Baker *et al.* (1995) paper, but we included the ambient CO_2 treatments for this comparison. Doubling the CO_2 concentration

increased biomass and grain yield by 25 and 32%, respectively, in those studies, but there was no CO_2 by temperature interaction. A subsequent rice experiment was conducted by Snyder (2000), with two cultivars of contrasting climatic origin, IR72 (tropical, *indica* type) and M103 (temperate, *japonica* type), grown in adjacent halves of each chamber. In that study, air temperatures followed diurnal temperature cycles as described. Snyder's results basically confirmed those described above, showing that optimum temperature for grain yield and HI was slightly different for the two ecotypes (25°C for the *japonica* M103 cultivar and 28°C for the *indica* IR72 cultivar); however, both ecotypes failed equally and completely in grain yield and HI at 35°C mean air temperature (the 40/30°C treatment). Thus, the tropical origin of the *indica* line did not give it any greater temperature tolerance. On the other hand, the *indica* line was more cold-sensitive, as it produced fewer spikelets at 28/18°C treatment, at which temperature the *japonica* type performed very well. The decrease in yield with above-optimum temperature was attributed to progressive decrease in filled grains per panicle, while grain size was nearly unaffected by temperature (Baker and Allen, 1993a; Snyder, 2000). The Snyder study confirmed that decline in the percentage of filled grains was the primary contributor to declining grain yield as temperature rose, especially at the higher failure points of 40/30°C (Fig. 1c). The temperature sensitivity of the percentage of filled grains was in agreement with the results published by Kim *et al.* (1996) and Matsui *et al.* (1997). At intermediate high temperatures between 31/21 and 40/30°C, shorter grain filling duration was an additional contributor to reduced grain yield, along with slightly lower total biomass accumulation (Snyder, 2000).

Red Kidney dry bean is a large-seeded type. Large-seeded *Phaseolus vulgaris* belong to the Andean ecotype group, which originates in the tropical highlands and is known to be heat-susceptible, when contrasted to small-seeded Mesoamerican ecotypes that originate from the lowlands (Sexton *et al.*, 1994). Our experiments clearly demonstrated that Red Kidney bean was very susceptible to elevated temperature, and was more sensitive than rice. In experiments by Prasad *et al.* (2002), the highest seed yield occurred at 28/18°C, with yield declining linearly as temperature increased, reaching zero yield at 37/27°C. Seed HI followed the same trend. Again, reproductive processes failed sooner than did dry matter accumulation. Leaf photosynthesis in saturating light was 30% less at 40/30°C than at 28/18°C. On the other hand, pollen production per flower was reduced above 31/21°C, and pollen viability was dramatically reduced above 34/24°C, falling to near zero at 37/27°C (Fig. 2a). The result was progressively

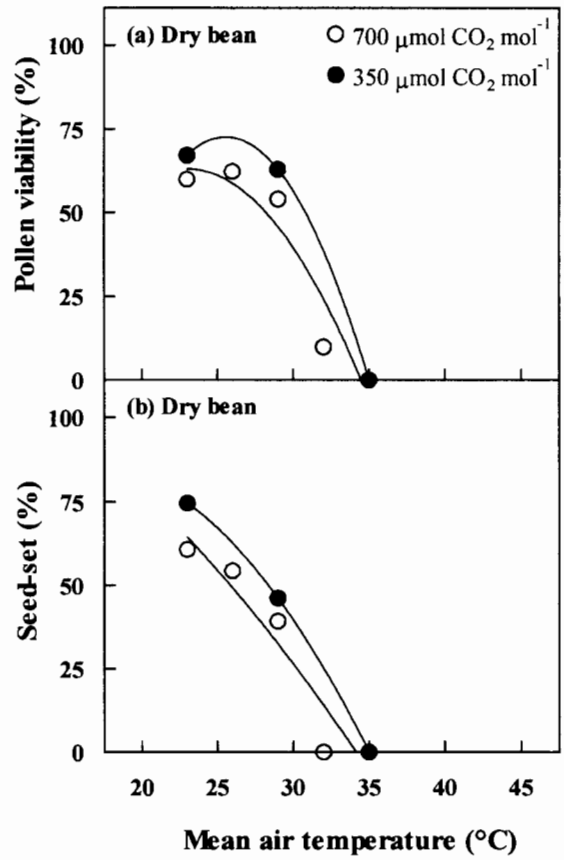

Fig. 2. (a) Pollen viability, and (b) seed-set percentage of dry bean cv. Montcalm as affected by air temperature and [CO_2] (Prasad et al., 2002).

decreased seed-set (percentage of locule sites becoming seeds) and progressive decrease in seeds per pod as temperature increased above 28/18°C (Fig. 2b). Decline in seed yield and HI originated not only from flower fertilization failures, but also from decreases in seed size above 31/21°C. The cardinal temperature points for optimum yield and complete failure of seed production were 3°C lower for dry bean than for rice. At 37/27°C, there was significant vegetative growth of bean, although less vigorous and somewhat heat-stressed, but there was no seed formation. Interestingly, there was a proliferation of thin parthenocarpic seedless pods about 4-5 cm long.

Soybean and peanut are generally viewed as heat-tolerant species, and this was reinforced in our experiments. Experiments by Prasad *et al.* (2003) showed that the optimum mean temperature for grain yield of peanut was either at or possibly below 26°C (32/22°C treatment), while experiments on soybean (Pan, 1996; Thomas, 2001; Baker *et al.*, 1989) were less definitive, leaving open the possibility that optimum temperature for soybean yield could be above 26°C. For both species, yield and harvest index were progressively reduced by increasing temperature but the response was more gradual and

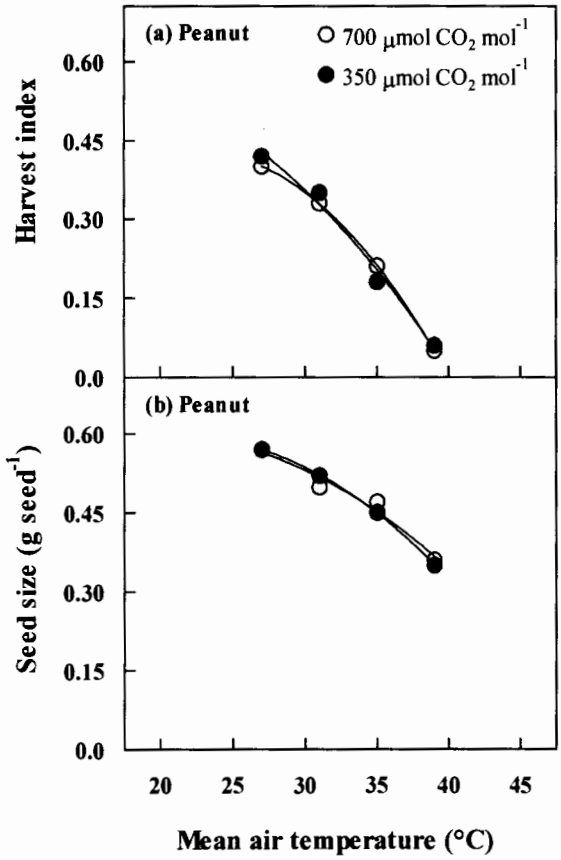

Fig. 3. (a) Seed harvest index, and (b) seed size of peanut cv. Georgia Green as affected by air temperature and [CO_2] (Prasad et al., 2003).

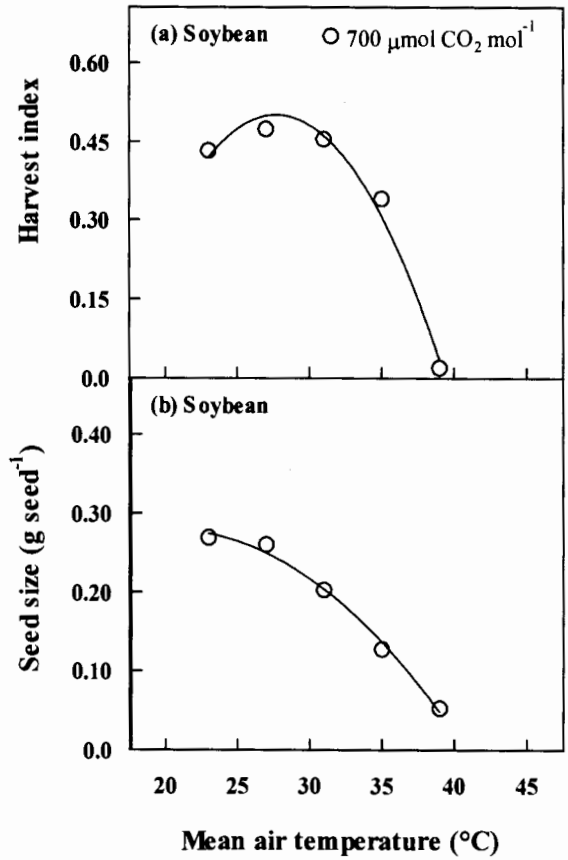

Fig. 4. (a) Seed harvest index, and (b) seed size of soybean cv. Bragg as affected by air temperature (Pan, 1996).

less dramatic (Figs. 3a and 4a) compared to rice or dry bean. Even at 39°C mean temperature (44/34°C treatments), there was a small amount of seed formation in both soybean and peanut. For both soybean and peanut, the seed harvest index (Figs. 3a and 4a) was optimum at 26°C and the decline in HI was more gradual, reaching zero at approximately 40°C (above the 44/34°C treatments). Thus, soybean and peanut have an optimum temperature that is very similar to rice, but they have nearly a 4°C higher failure point (40 vs. 36°C). Decline in grain yield of soybean and peanut was more gradual than for rice, a decline that we attributed to multiple causes. While rice tended to hold grain size almost constant until it failed, Figures 3b and 4b show that seed size was largest at 23°C (28/18°C) for soybean and at 26°C (32/22°C) for peanut (although that was the coolest treatment tested), and size was progressively reduced until 39°C (44/34°C). In rice, the failure was almost exclusively related to pollination failures with relatively small reduction in either filling period or grain size. For the grain legumes, yield decline was attributed to less dramatic pollination failures along with progressive reduction in grain size. Prasad *et al.* (2003) reported that pollen viability (Fig. 5a) and seed-set percentage (Fig. 5b) of peanut maintained well between 26°C (32/22°C) to 32°C (36/26°C), but were progressively decreased above 32°C (36/26°C), reaching zero at about 39°C (44/34°C). While no pollination data were collected on soybean, we suspect similar behavior in view of the similar decline in HI and seed size.

Effects of elevated CO_2 were beneficial as expected. However, for all four species, there were no beneficial interactions of temperature by CO_2 on reproductive processes and yield. Elevated CO_2 increased yield due to a greater number of reproductive sites (flowers, panicles) as a result of greater vegetative growth (e.g. tillering and branching). Averaged over non-failure temperatures and experiments, grain yield increases from doubling CO_2 were 32, 24, 29, and 30% for rice, dry bean, soybean, and peanut, respectively. But at above optimum temperatures, the enhancement due to elevated CO_2 became irrelevant as stressful temperatures caused progressively lower yields. Temperature increase above optimum led to a decrease in pollen production, pollen viability, seed-set, seed yield and harvest index in all four crop species. There was a negative interaction between

temperature and CO_2 on seed-set of dry bean (Fig. 2b). This is consistent with negative interaction found by Kim *et al.* (1996) and Matsui *et al.* (1997) for rice, although we did not see any interactions on rice HI or yield. Elevated CO_2 typically increases canopy and seed temperatures by 1 to 2°C associated with reduced stomatal conductance at elevated CO_2.

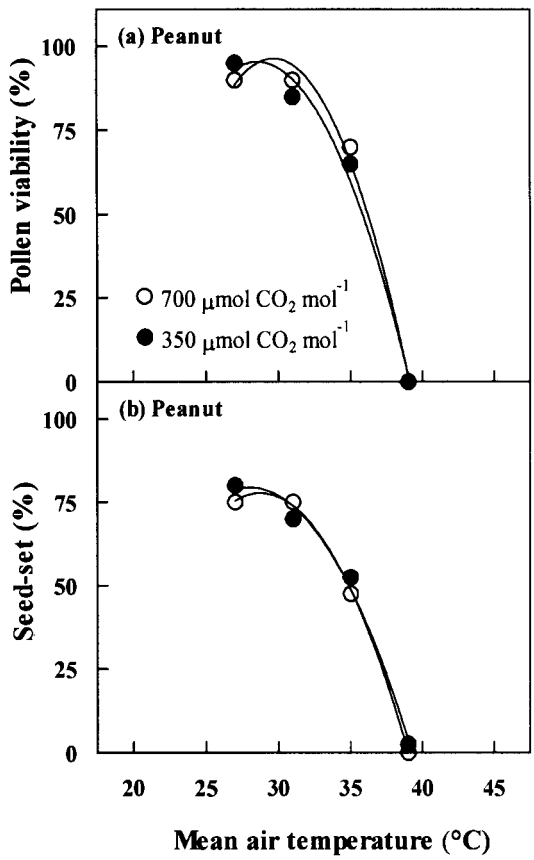

Fig. 5. (a) Pollen viability, and (b) seed-set percentage of peanut cv. Georgia Green as affected by air temperature and [CO_2] (Prasad et al., 2003).

The increased canopy and seed temperatures actually caused earlier failure in reproductive processes, as observed in dry bean (Prasad *et al.*, 2002), rice (Matsui *et al.*, 1997), and grain sorghum (Prasad *et al.*, 2004). In these three crop species, the maximum temperature which caused complete reproductive failure was about 2°C lower at elevated CO_2 compared to ambient CO_2.

We conclude that increases in air temperature anticipated with global climate change will adversely impact reproductive processes and seed yield of grain crops, and that there are no beneficial interactions of elevated temperature and CO_2. To the contrary, there are indications of negative interactions of elevated temperature and CO_2 for some species associated with the CO_2-induced increases in canopy temperature.

Acknowledgments

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