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Temperature extremes: Effect on plant growth and development

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ABSTRACT

Temperature is a primary factor affecting the rate of plant development. Warmer temperatures expected with climate change and the potential for more extreme temperature events will impact plant productivity. Pollination is one of the most sensitive phenological stages to temperature extremes across all species and during this developmental stage temperature extremes would greatly affect production. Few adaptation strategies are available to cope with temperature extremes at this developmental stage other than to select for plants which shed pollen during the cooler periods of the day or are indeterminate so flowering occurs over a longer period of the growing season. In controlled environment studies, warm temperatures increased the rate of phenological development; however, there was no effect on leaf area or vegetative biomass compared to normal temperatures. The major impact of warmer temperatures was during the reproductive stage of development and in all cases grain yield in maize was significantly reduced by as much as 80–90% from a normal temperature regime. Temperature effects are increased by water deficits and excess soil water demonstrating that understanding the interaction of temperature and water will be needed to develop more effective adaptation strategies to offset the impacts of greater temperature extreme events associated with a changing climate.

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1. Introduction

Rate of plant growth and development is dependent upon the temperature surrounding the plant and each species has a specific temperature range represented by a minimum, maximum, and optimum. These values were summarized by Hatfield et al. (2008, 2011) for a number of different species typical of grain and fruit production. The expected changes in temperature over the next 30–50 years are predicted to be in the range of 2–3 °C Intergovernmental Panel Climate Change (IPCC) (2007). Heat waves or extreme temperature events are projected to become more intense, more frequent, and last longer than what is being currently been observed in recent years (Meehl et al., 2007). Extreme temperature events may have short-term durations of a few days with temperature increases of over 5 °C above the normal temperatures. Extreme events occurring during the summer period would have the most dramatic impact on plant productivity; however, there has been little research conducted to document these effects as found by Kumudini et al. (2014). A recent review by Barlow et al. (2015) on the effect of temperature extremes, frost and heat, in wheat (*Triticum aestivum* L.) revealed that frost caused sterility and abortion of formed grains while excessive heat caused reduction in grain number and reduced duration of the grain-filling period. Analysis by Meehl et al. (2007) revealed that daily minimum temperatures will increase more rapidly than daily maximum temperatures leading to the increase in the daily mean temperatures and a greater likelihood of extreme events and these changes could have detrimental effects on grain yield. If these changes in temperature are expected to occur over the next 30 years then understanding the potential impacts on plant growth and development will help develop adaptation strategies to offset these impacts.

1.1. Temperature responses

Responses to temperature differ among crop species throughout their life cycle and are primarily the phenological responses, i.e., stages of plant development. For each species, a defined range of maximum and minimum temperatures form the boundaries of observable growth. Vegetative development (node and leaf appearance rate) increases as temperatures rise to the species optimum level. For most plant species, vegetative development usually has a higher optimum temperature than for reproductive development. Cardinal temperature values for selected annual (non-perennial) crops are given in Hatfield et al. (2008, 2011) for different species. If we depict the range of temperatures in the following diagram (Fig. 1) then the definition of extreme temperatures affecting plant response will be species dependent. For

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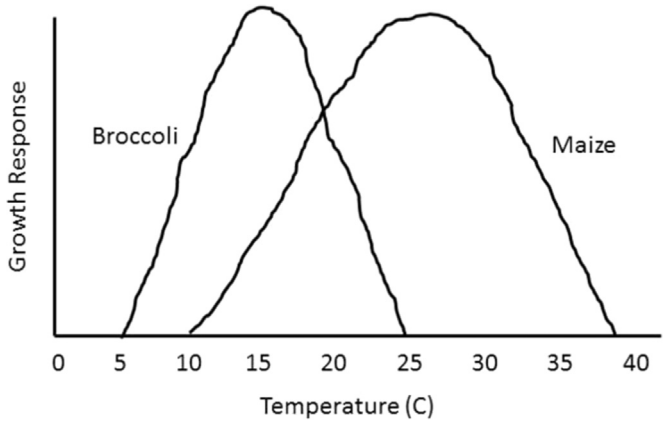


Fig. 1. Temperature response for maize and broccoli plants showing the lower, upper and optimum temperature limits for the vegetative growth phase.

example, an extreme event for maize (*Zea mays* L.) will be warmer than for a cool season vegetable (broccoli, *Brassica oleracea* L.) where the maximum temperature for growth is 25 °C compared to 38 °C. In understanding extreme events and their impact on plants we will have to consider the plant temperature response relative to the meteorological temperature.

Faster development of non-perennial crops results in a shorter life cycle resulting in smaller plants, shorter reproductive duration, and lower yield potential. Temperatures which would be considered extreme and fall below or above specific thresholds at critical times during development can significantly impact productivity. Photoperiod sensitive crops, e.g., soybean, would also interact with temperature causing a disruption in phenological development. In general, extreme high temperatures during the reproductive stage will affect pollen viability, fertilization, and grain or fruit formation (Hatfield et al., 2008, 2011). Chronic exposures to extreme temperatures during the pollination stage of initial grain or fruit set will reduce yield potential. However, acute exposure to extreme events may be most detrimental during the reproductive stages of development.

The impacts of climate change are most evident in crop productivity because this parameter represents the component of greatest concern to producers, as well as consumers. Changes in the length of the growth cycle are of little consequence as long as the crop yield remains relatively consistent. Yield responses to temperature vary among species based on the crop's cardinal temperature requirements. Warming temperatures associated with climate change will affect plant growth and development along with crop yield.

1.2. Temperature extremes in climate

One of the more susceptible phenological stages to high temperatures is the pollination stage. Maize pollen viability decreases with exposure to temperatures above 35 °C (Herrero and Johnson, 1980; Schoper et al., 1987; Dupuis and Dumas, 1990). The effect of temperature is enhanced under high vapor pressure deficits because pollen viability (prior to silk reception) is a function of pollen moisture content which is strongly dependent on vapor pressure deficit (Fonseca and Westgate, 2005). During the endosperm division phase, as temperatures increased to 35 °C from 30 °C the potential kernel growth rate was reduced along with final kernel size, even after the plants were returned to 30 °C (Jones et al., 1984). Exposure to temperatures above 30 °C damaged cell division and amyloplast replication in maize kernels which reduced the size of the grain sink and ultimately yield (Commuri and Jones, 2001). Rice (*Orzya sativa* L.) shows a similar temperature response to maize because pollen viability and production declines as daytime maximum temperature (T_{max}) exceeds 33 °C and ceases when T_{max} exceeds 40 °C (Kim et al., 1996). Current cultivars of rice flower near mid-day which makes Tmax a good indicator of heat-stress on spikelet sterility. These exposure times occur quickly after anthesis and exposure to temperatures above 33 °C within 1 – 3 h after anthesis (dehiscence of the anther, shedding of pollen, germination of pollen grains on stigma, and elongation of pollen tubes) cause negative impacts on reproduction (Satake and Yoshida, 1978). Current observations in rice reveal that anthesis occurs between about 9 to 11 am in rice (Prasad et al., 2006b) and exposure to high temperatures may already be occurring and will increase in the future. There is emerging evidence that differences exist among rice cultivars for flowering times during the day (Sheehy et al., 2005). Given the negative impacts of high temperatures on pollen viability, recent observations from Shah et al. (2011) suggest flowering at cooler times of the day would be beneficial to rice grown in warm environments. They proposed that variation in flowering times during the day would be a valuable phenotypic marker for high-temperature tolerance. As daytime temperatures increased from 30 to 35 °C, seed set on male-sterile, female fertile soybean (*Glycine max* (L.) Merr.) plants decreased (Wiebbecke et al., 2012). This confirms earlier observations on partially male-sterile soybean in which complete sterility was observed when the daytime temperatures exceeded 35 °C regardless of the night temperatures and concluded that daytime temperatures were the primary factor affecting pod set Caviness and Fagala (1973). Crop sensitivity to temperature extremes depends upon the length of anthesis. Maize, for example, has a highly compressed phase of anthesis for 3 – 5 days, while rice, sorghum (*Sorghum bicolor* L. Moench.) and other small grains may extend anthesis over a period of a week or more. Inn soybean, peanut (*Arachis hypogaea* L.), and cotton (*Gossypium hirsutum* L.) anthesis occurs over several weeks and avoid a single occurrence of an extreme event affecting all of the pollening flowers. For peanut (and potentially other legumes) the sensitivity to elevated temperature for a given flower, extends from 6 days prior to opening (pollen cell division and formation) up through the day of anthesis (Prasad et al., 2001). Therefore, several days of elevated temperature may affect fertility of flowers in their formative 6-day phase or anthesis. Singh et al. (2015) found differences in the threshold temperature for grain sorghum among genotypes and differences in the percentage of seed set in response to high temperatures. Pollination processes in other cereals, maize and sorghum, may have a similar sensitivity to elevated daytime temperature as rice. Rice and sorghum have exhibited similar sensitivities of grain yield, seed harvest index, pollen viability, and success in grain formation in which pollen viability and percent fertility is first reduced at instantaneous hourly air temperature above 33 °C and reaches zero at 40 °C (Kim et al., 1996; Prasad et al., 2006a, 2006b). Diurnal max/min day/night temperatures of 40/30 °C (35 °C mean) cause zero yield for those two species with the same expected response for maize.

1.3. Annual crops

Projected air temperature increases throughout the remainder of the 21st century suggests that grain yields will continue to decrease for the major crops because of the increase temperature stress on all major grain crops (Hatfield et al., 2011). Beyond a certain point, higher air temperatures adversely affect plant growth, pollination, and reproductive processes (Klein et al., 2007; Sacks and Kucharik, 2011). However, as air temperatures rise beyond the optimum, instead of falling at a rate commensurate with the temperature increase, crop yield losses accelerate. For example, an analysis by Schlenker and Roberts (2009) indicated yield

growth for corn, soybean, and cotton would gradually increase with temperatures up to 29°C to 32°C and then sharply decrease with temperature increases beyond this threshold.

Increases of temperature may cause yield declines between 2.5% and 10% across a number of agronomic species throughout the 21st century (Hatfield et al., 2011). Other evaluations of temperature on crop yield have produced varying outcomes. Lobell et al. (2011) showed estimates of yield decline between 3.8% and 5%; and Schlenker and Roberts (2009) used a statistical approach to estimate wheat, corn, and cotton yield declines of 36% to 40% under a low CO_2 emissions scenario, and between 63% to 70% for high CO_2 emission scenarios. These estimates of yield loss did not consider the positive effects of rising atmospheric CO_2 on crop growth, variation among crop genetics, impact of biotic stresses on crop growth and yield, or the use of adaptive management strategies, e.g., fertilizers, rotations, tillage, or irrigation. These analyses assumed that air temperature increased without regard to the potential negative effects of temperature extremes.

The current evaluations of the impact of changing temperature have focused on the effect of average air temperature changes; however, increases in minimum air temperature may be more significant in their effect on growth and phenology (Hatfield et al., 2011). Minimum air temperatures are more likely to increase under climate change (Knowles et al., 2006). While maximum temperatures are affected by local conditions, especially soil water content and evaporative heat loss as soil water evaporates (Alfaro et al., 2006), minimum air temperatures are affected by mesoscale changes in atmospheric water vapor content. Hence, in areas where changing climate is expected to cause increased rainfall or where irrigation is predominant, large increases of maximum temperatures are less likely to occur than in regions prone to drought. Minimum air temperatures affect nighttime plant respiration rates and can potentially reduce biomass accumulation and crop yield (Hatfield et al., 2011). Welch et al. (2010) found higher minimum temperatures reduced grain yield in rice, while higher maximum temperature raised yields; because the maximum temperature seldom reached the critical optimum temperature for rice. However, under the scenario of future temperatures increases, they found maximum temperatures could decrease yields if they are near the upper threshold limit.

Similar responses have been found in annual specialty crops in which temperature is the major environmental factor affecting production with specific stresses, such as periods of hot days, overall growing season climate, minimum and maximum daily temperatures, and timing of stress in relationship to developmental stages having the greatest effect (Ghosh et al., 2000; Pressman et al., 2002; McKeown et al., 2005; Sønsteby and Heide, 2008; Dufault et al., 2009). When plants are subjected to mild heat stress (1 °C to 4 °C above optimal growth temperature), there was moderately reduced yield (Sato, 2006; Timlin et al., 2006; Wagstaffe and Battey, 2006; Tesfaendrias et al., 2010). In these plants, there was an increased sensitivity heat stress 7 to 15 days before anthesis, coincident with pollen development. Subjecting plants to a more intense heat stress (generally greater than 4 °C above optimum) resulted in severe yield loss extending to complete crop failure (Ghosh et al., 2000; Sato et al., 2000; Kadir et al., 2006; Gote and Padghan, 2009; Tesfaendrias et al., 2010). Tomatoes under heat stress fail to produce viable pollen while their leaves remain active. The non-viable pollen does not pollinate flowers causing failure in fruit set (Sato et al., 2000). If the same stressed plants are cooled to normal temperatures for 10 days before pollination, and then returned to high heat, they are able to develop fruit. There are some heat tolerant tomatoes which perform better than others related to their ability to successful pollinate even under adverse conditions (Peet et al., 2003; Sato, 2006).

Perennial crops have a more complex relationship to temperature than annual crops. Many perennial crops have a chilling requirement in which plants must be exposed to a number of hours below some threshold temperature before flowering can occur. For example, chilling hours for apple (*Malus domestica* Borkh.) range from 400 to 2900 h (5 – 7 °C base, Hauagge, 2010) while cherry trees (*Prunus avium)* require 900 to 1500 h with the same base temperature (Seif and Gruppe, 1985). Grapes (*Vitis vinifera* L.) have a lower chilling threshold that other perennial plants with some varieties being as low at 90 h (Reginato et al., 2010). Increasing winter temperatures may prevent chilling hours from being obtained and projections of warmer winters in California revealed that by mid-21st century, plants requiring more than 800 h may not be exposed to sufficient cooling except in very small areas of the central Valley (Luedeling et al., 2009). Climate change will impact the chilling requirements for fruits and nut trees. Hatfield et al. (2014) showed that under a warming climate, adequate chilling hours for perennial crops for fruit development may not be met. Innovative adaptation strategies will be required to overcome this effect because of the long time requirements for genetic selection and fruit production once perennial crops are established.

Perennial plants are also susceptible to exposure to increasing temperatures similar to annual plants. These responses and the magnitude of the effects are dependent upon individual species. Exposure to high temperatures, > 22 °C, for apples during reproduction increases the fruit size and soluble solids but decreases firmness as a quality parameter (Warrington et al., 1999). In cherries, increasing the temperature 3 °C above the 15 °C optimum mean temperature decreases fruit set (Beppu et al., 2001). Optimum temperature range in citrus (*Citrus sinensis* L. Osbeck) is 22 – 27 °C and temperatures greater than 30 °C increased fruit drop (Cole and McCloud, 1985). During fruit development when the temperatures exceed the optimum range of 13 – 27 °C with temperatures over 33 °C there is a reduction in Brix (sugar content), acid content, and fruit size in citrus (Hutton and Landsberg, 2000). Temperature stresses on annual and perennial crops have an impact on all phases of plant growth and development.

Exposure of plants to extreme temperatures will limit the ability of the plant to produce fruit due to disruption of the pollination process. The magnitude of this impact varies among species; however, there is a consistent negative impact on plants. One aspect of high temperature extremes often overlooked is the effect of extreme events on the atmospheric water vapor demand. If we plot the saturation vapor pressure (e_*) relative to air temperature we see an exponential increase of e_* with temperature

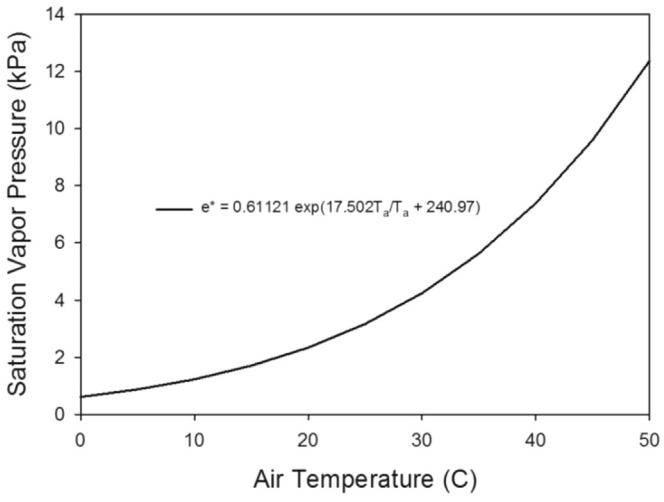


Fig. 2. Saturation vapor pressure relative to air temperature showing the exponential increase in saturation vapor pressure with temperature.

(Fig. 2). The following equation to represents the energy balance of a leaf:

$$S_t(1-a_l)+L_d-\varepsilon\sigma T_l^4=\frac{pC_p(T_l-T_a)}{r_a}+\frac{pC_p(e^*-e_a)}{r(r_s+r_a)} \quad (1)$$

where S_t is the incoming solar radiation (W m^{-2}), α_l is the albedo of the leaf or canopy, L_d is the incoming long-wave radiation (W m^{-2}), ε is the emissivity of the leaf or canopy, σ is the Stefan – Boltzmann constant, T_l the leaf or canopy temperature, r_a is the aerodynamic conductance (m s^{-1}), and r_s the canopy conductance (m s^{-1}), then we see how changing e* would affect the energy balance. An increasing water vapor demand will cause more water to be transpired by the leaf until the water supply becomes limited and the stomatal conductance will decrease leading to a higher leaf temperatures and a reduction in photosynthesis. If the plant is exposed to extreme temperatures, water stress could occur quickly because the plant lacks sufficient capacity to extract water from the soil profile to meet the increased atmospheric demand. The linkages among these parameters have been discussed in detail in a review by Hatfield and Prueger (2011). The effects of temperature extremes on the plant could be from the combined effect of the warm air temperatures and the increasing atmospheric demand.

The effects of extreme temperature from either acute or chronic exposure can have large impacts on plant growth and development. We report the results of two different studies designed to evaluate the effects of acute and chronic exposure to extreme high temperatures of maize throughout its life cycle.

2. Experimental procedures

Experiments were conducted in the rhizotron facility located in the National Laboratory for Agriculture and the Environment at Ames, Iowa. This facility was described by Logsdon et al. (2002) where each chamber contains three $1 \times 1 \times 1.5$ m deep Monona silt loam (fine-silty, mixed mesic Typic.Hapludoll) soil monoliths. These chambers allow for the control of light intensity, daylength, air temperature, and relative humidity through a computer controlled system programmed to to replicate the average weekly temperatures and daylength for Ames, Iowa from April 1 through October 30. We used the 30 year normal temperatures and the weekly precipitation amounts to simulate these averages. Each soil monolith has a drainage system to allow water to drain through the soil profile. Soil moisture sensors measured the upper 10 cm of the soil profile. In the first experiment, the maize hybrid Northrup King N68B 3111 was planted in with two rows of five plants in each row to simulate a population density of 100,000 plants ha^{-1} similar to a typical plant population for maize production in the Midwest. All monolith blocks were treated with the equivalent of 180 kg ha^{-1} of nitrogen with all other nutrients provided to be adequate for maize production. Light intensities were set at approximately 1100 μmoles m^{-2} PAR. Water was applied to each block weekly to simulate the average amount of precipitation for that week. One block was treated with normal amounts of precipitation, a second block at 1.25 of normal, and the third block at 0.75 of normal to simulate excess and water deficit conditions, respectively. Visual observations were made of plant growth during the season and in one chamber the air temperatures were increased by 5 °C for one week at the V6, V12, and pollination stage. The chamber with the high temperature exposures then had minimum temperatures increased by 3 °C for the period from the end of pollen shed until maturity of the crop. Numbers of leaves, leaf length and maximum leaf width were measured throughout the growing season to determine phenological development and leaf area. At maturity, each plant was harvested from the soil block and the vegetative biomass and grain amounts determined for each plant and then averaged for the block to determine the production.

In the second experiment, one of the chambers was maintained at the average weekly temperature for Ames throughout the growing season with normal precipitation applied weekly to the monoliths while the second chamber was maintained at 4 °C above average throughout the growing season. In this experiment six plants were planted in each row in a monolilth and two rows apart were planted and the thinned at the one-leaf stage to achieve a plant density was 120,000 plants m^{-2}. Chambers were calibrated to ensure the same atmospheric water deficit was maintained in each chamber so that the only effect on plant growth would be temperature with no interactions from imposed water deficits. The hybrid, Dekalb RX730, adapted to the Ames environment was used as the experimental hybrid. Weekly measurements were made of the number of leaf collars and leaf tips to record the phenological development on 10 plants in each monolith. Measurements were made of the length and maximum width of each new fully emerged leaf to estimate leaf area by multiplying length × width × 0.67 using the procedure described by Hatfield et al. (1976). These measurements continued until all leaves emerged. At maturity, all plants were harvested for total vegetative biomass and grain yield and individually recorded. This experiment was replicated twice over time with the same hybrid and experimental procedures.

To compare between the stresses imposed on the plants, *T*-tests between the treatments were used to evaluate the treatment differences which was adequate for this experiment.

3. Results and discussion

In experiment 1 with extreme temperatures imposed at different stages, there was no difference in phenological development and leaf area was the same among water level treatments and chambers where extreme events were imposed. However, there was a significant difference in the total vegetative dry weights between extreme temperature events (Table 1).

The normal precipitation soil water treatment produced the highest biomass and grain yield in both temperature treatments and either deficit water or excess soil water reduced biomass and grain yield in the normal temperature regime (Table 1). In the

Table 1
Total Vegetative biomass and grain weights for maize exposed to temperature extremes and soil water differences in a controlled environment chamber.

Chamber	Soil water treatment	Total vegetative dry matter (g m^{-2})	Grain yield (g m^{-2})
Normal temperature	Normal precipitation	3739.5	1573.5
Normal temperature	0.75 Normal precipitation	3000.7	707.0
Normal temperature	1.25 Normal precipitation	2708.1	944.1
Extreme temperature	Normal precipitation	1744.8	823.4
Extreme temperature	0.75 Normal precipitation	1282.6	805.6
Extreme temperature	1.25 Normal precipitation	1081.8	353.9

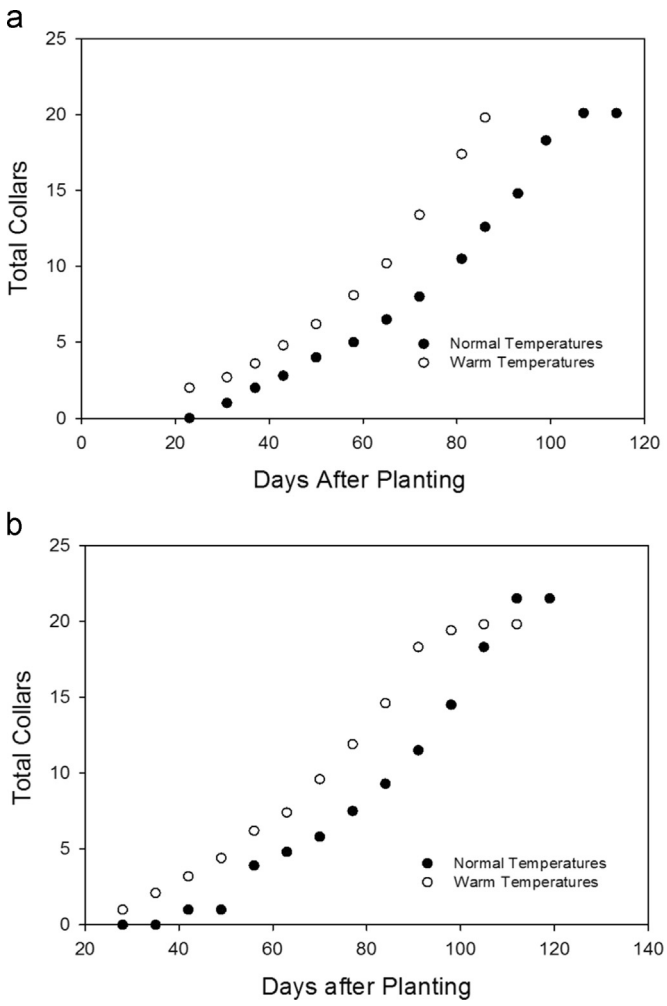


Fig. 3. Weekly progress in leaf collars in the corn hybrid RX730 grown under normal air temperatures for Ames, IA, and under normal + 3 °C air temperatures.

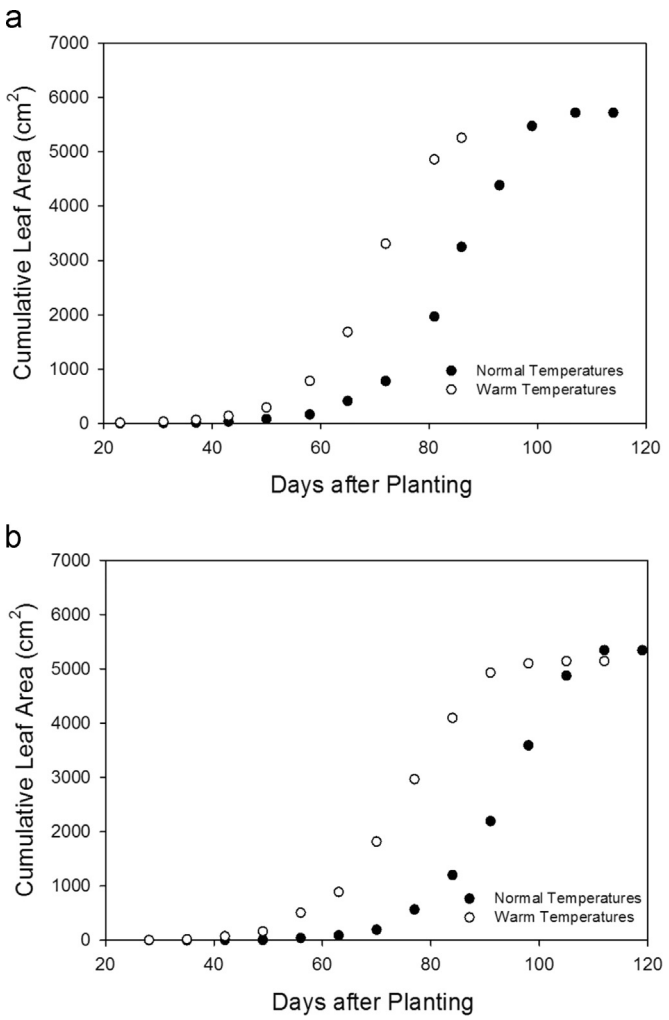


Fig. 4. Weekly progress in cumulative leaf area for the corn hybrid RX730 grown under normal air temperatures for Ames, IA and under normal + 3 °C air temperatures for two replicates with time, graph a is the first experiment and b the second experiment.

chamber with exposure to extreme temperature events there was a significant reduction in biomass and grain yield for any comparable soil water regime. The largest effect of the temperature extremes was found under the conditions of excess water in which biomass and yield were reduced by nearly two-thirds. There was no effect of temperature treatment on phenological development and all plants were at the same stage of development through the pollination stage. Increased night temperatures significantly increased the rate of senescence and maturity was achieved in these plants 15 days earlier than in the normal temperature chamber. The effects of high minimum temperatures increased the rate of senescence and decreased the ability of the plant to efficiently produce grain. The interactions of temperature and soil water content need to be understood in order develop effective adaptation practices for agronomic systems in response to climate extremes.

In experiment 2 where one chamber was maintained at 4 °C above normal for the entire growing season there were differences in the phenological development. There was no significant difference in the number of total leaf collars for the different temperature regimes, only the rate of leaf appearance was different. The same response was observed for both experiments (Fig. 3). In experiment 2, we measured the leaf area on each leaf as it reached maximum size and observed no significant difference in cumulative leaf area between temperature treatments and the same total leaf area was observed for the two experiments (Fig. 4). The effect of warm temperatures was observed only in the rate of development of the plants until the beginning of the reproductive stage. Similar leaf area and number of leaves produced the same amount of total vegetative biomass with no significant differences in biomass between treatments and experiments (Table 2). Warm temperatures increased the rate of senescence during grain-fill and reduced final grain yield (Table 2). Grain production was significantly reduced in the warm chamber in both experiments. The difference in the final yield between the two experiments was that experiment two was terminated at the R5 stage before final maturity because of a failure in the light system in the warm chamber; however, the magnitude of the yield impact was the same

Table 2
Total vegetative biomass and grain yield for hybrid RX730 grown under normal and warm temperatures for two experimental replicates using Ames, Iowa, normal conditions.

Replicate	Parameter	Normal temperatures	Warm temperatures
1	Total vegetative biomass ($g\ m^{-2}$)	920.3	1188.0
1	Grain yield ($g\ m^{-2}$)	1870.0	213.9
2	Total vegetative biomass ($g\ m^{-2}$)	1007.0	1122.1
2	Grain yield ($g\ m^{-2}$)	471.2	59.9

between experiments. The warmer temperatures showed the same effect as the previous experiment where the rate of senescence increased. To evaluate the effect of the warmer temperatures we evaluated the number of hours in the life cycle that exceeded 30 °C in the period from emergence to tasseling and from tasseling until maturity. In the first cycle, the normal temperature chamber had 2129 total hours between 10 and 30 °C with no hours above 30 °C while the warm chamber had 1449 h between 10 and 30 °C and 233 h above 30 °C during the grain-filling period. In the second cycle the normal temperature chamber had 1960 h between 10 and 30 °C and 12 above 30 °C while the warm temperature chamber had 1628 h between 10 and 30 °C and 156 above 30 °C. The exposure to higher temperatures during the grain-filling period includes temperatures which were warmer during the night. The effect of increasing minimum temperatures during the reproductive period produced negative impacts on yield. Although the rates of development were faster in the vegetative stage of development the shortening of this period was not detrimental to yield because there was no negative effect on leaf area or biomass because the exposure to temperatures above the optimum is negligible (Fig. 1). This aspect needs to be evaluated to more completely determine the impact of warmer temperatures during the complete live cycle of plants. The effects of warmer temperatures during the vegetative stage may have less of a negative impact because the temperatures do not exceed the optimum.

4. Conclusions

Temperature effects on plant growth and development is dependent upon plant species. Under an increasing climate change scenario there is a greater likelihood of air temperatures exceeding the optimum range for many species. Cool season species will have a constrained growing season because of the potential of average temperatures exceeding their range as illustrated by broccoli in Fig. 1. The temperature response of different species has been evaluated by Prasad et al. (2001, 2002, 2003, 2006a, 2006b, 2008). The effect of temperature extremes on plant growth and development has not been extensively studied with the major effect during the pollination phase. Exposure of plants to temperature extremes at the onset of the reproductive stage has a major impact on fruit or grain production across all species. One potential strategy to minimize this impact is to select varieties which shed their pollen in the early morning when temperatures are cooler (Shah et al., 2011). The synthesis by Barlow et al. (2015) on heat shock from high temperatures demonstrates the need to increase our understanding of the impact of temperatures above the threshold on the ability of the plant to set grain and also change the duration of the grain-filling period. The expectation of greater occurrences of temperature extremes will continue to have increasing negative impacts on plant production.

The effects of increased temperature exhibit a larger impact on grain yield than on vegetative growth because of the increased minimum temperatures. These effects are evident in an increased rate of senescence which reduces the ability of the crop to efficiently fill the grain or fruit. Observations in controlled environment studies show that maize grain yield is greatly reduced by above normal temperatures during the grain-filling period. Temperature effects interact with the soil water status which would suggest that variation in precipitation coupled with warm temperatures would increase the negative effects on grain production. These observations and the previous results from the literature suggest that more research needs to be conducted to quantify the interactions between temperature and soil water availability across germplasm within a species and among species to determine potential adaptation strategies to offset negative effects of extreme temperature events.

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References

Alfaro, E.J., Gershunov, A., Cayan, D., 2006. Prediction of summer maximum and minimum temperature over the central and western United States: the roles of soil moisture and sea surface temperature. J. Clim. 19, 1407–1421.
Barlow, K.M., Christy, B.P., O'Leary, G.J., Riffkin, P.A., Nuttall, J.G., 2015. Simulating the impact of extreme heat and frost events on wheat crop production: a review. Field Crops Res. 171, 109–119.
Beppu, K., Ikeda, T., Kataoka, I., 2001. Effect of high temperature exposure time during flower bud formation on the occurrence of double pistils in''-satohnishiki' sweet cherry. Sci. Horticul. 87, 77–84.
Caviness, C.E., Fagala, B.L., 1973. Influence of temperature on partially male-sterile soybean strain. Crop Sci. 13, 503–504.
Cole, P., McCloud, P., 1985. Salinity and climatic effects on the yields of citrus. Aust. J. Exp. Agric. 25, 711–717.
Commuri, P.D., Jones, R.D., 2001. High temperatures during endosperm cell division in maize: a genotypic comparison under *in vitro* and field conditions. Crop Sci. 41, 1122–1130.
Dufault, R.J., Ward, B., Hassell, R.L., 2009. Dynamic relationships between field temperatures and romaine lettuce yield and head quality. Sci. Hortic. 120, 452–459.
Dupuis, L., Dumas, C., 1990. Influence of temperature stress on *in vitro* fertilization and heat shock protein synthesis in maize (*Zea mays* L.) reproductive systems. Plant Physiol. 94, 665–670.
Fonseca, A.E., Westgate, M.E., 2005. Relationship between desiccation and viability of maize pollen. Field Crops Res. 94, 114–125.
Ghosh, S.C.A., Koh, ichiro, Kusutani, Akihito, Toyota, Masanori, 2000. Effects of temperature at different growth stages on nonstructural carbohydrate, nitrate reductase activity and yield of potato. Environ. Control Biol. 38, 197–206.
Gote, G.N., Padghan, P.R., 2009. Studies on different thermal regimes and thermal sensitivity analysis of tomato genotypes. Asian J. Environ. Sci. 3, 158–161.
Hatfield, J.L., Prueger, J.H., 2011. Agroecology: Implications for Plant Response to Climate Change. In: Yadav, S.S., Redden, R.J., Hatfield, J.L., Lotze-Campen, H., Hall, A.E. (Eds.), Wiley-Blackwell, West Sussex, UK, pp. 27–43.
Hatfield, J.L., Stanley, C.D., Carlson, R.E., 1976. Evaluation of an electronic foliometer to measure leaf area in corn and soybean. Agron. J. 68, 434–436.
Hatfield, J.L., Boote, K.J., Fay, P., Hahn, L., Izaurralde, R.C., Kimball, B.A., Mader, T., Morgan, J., Ort, D., Polley, W., Thomson, A., Wolfe, D., 2008. Agriculture In:. The Effects of Climate Change on Agriculture, Land Resources, Water Resources, and Biodiversity in the United States.
Hatfield, J.L., Boote, K.J., Kimball, B.A., Ziska, L.H., Izaurralde, R.C., Ort, D., Thomson, A.M., Wolfe, D.W., 2011. Climate impacts on agriculture: implications for crop production. Agron. J. 103, 351–370.
Hatfield, J.L., Takle, G., Grothjahn, R., Holden, P., Izaurralde, R.C., Mader, T., Marshall, E., Liverman, D., 2014. Ch. 6. Agriculture. Climate Change Impacts in the United States: The Third National Climate Assessment. In: Melillo, J.M., Richmond, T.C., Yohe, G.W. (Eds.), , pp. 150–174. http://dx.doi.org/10.7930/J02Z13FR.
Hauagge, R., 2010. ''IPR julieta', a new early low chill requirement apple cultivar. Acta Hortic. (ISHS) 872, 193–196.
Herrero, M.P., Johnson, R.R., 1980. High temperature stress and pollen viability in maize. Crop Sci. 20, 796–800.
Hutton, R.J., Landsberg, J.J., 2000. Temperature sums experienced before harvest partially determine the post-maturation juicing quality of oranges grown in the Murrumbidgee Irrigation Areas (MIA) of New South Wales. J. Sci. Food Agric. 80, 275–283.
Intergovernmental Panel Climate Change (IPCC), 2007. Climate Change 2007: Impacts, Adaptation and Vulnerability: Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, U.K. and New York, NY.
Jones, R.J., Ouattar, S., Crookston, R.K., 1984. Thermal environment during endosperm cell division and grain filling in maize: effects on kernel growth and development in vitro. Crop Sci. 24, 133–137.
Kadir, S., Sidhu, G., Al-Khatib, K., 2006. Strawberry (Fragaria × ananassa duch.) growth and productivity as affected by temperature. HortScience 41, 1423–1430.
Kim, H.Y., Horie, T., Nakagawa, H., Wada, K., 1996. Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. II. The effect of yield and its component of Akihikari rice. Jpn. J. Crop Sci. 65, 644–651.

Klein, J.A., Harte, J., Zhao, X.-Q., 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan plateau. Ecol. Appl. 17, 541–557.
Knowles, N., Dettinger, M.D., Cayan, D.R., 2006. Trends in snowfall versus rainfall in the western United States. J. Clim. 19, 4545–4559.
Kumudini, S., Andrade, F.H., Boote, K.J., Brown, G.A., Dzotsi, K.A., Edmeades, G.O., Gocken, T., Goodwin, M., Halter, A.L., Hammer, G.L., Hatfield, J.L., Jones, J.W., Kemanian, A.R., Kim, S.-H., Kiniry, J., Lizaso, J.I., Nendel, C., Nielsen, R.L., Parent, B., StÖckle, C.O., Tardieu, F., Thomison, P.R., Timlin, D.J., Vyn, T.J., Wallach, D., Yang, H.S., Tollenaar, M., 2014. Predicting maize phenology: intercomparison of functions for developmental response to temperature. Agron. J. 106, 2087–2097.
Lobell, D.B., Schlenker, W., Costa-Roberts, J., 2011. Climate trends and global crop production since 1980. Science 333, 616–620.
Logsdon, S.D., Kaspar, T.C., Meek, D.W., Prueger, J.H., 2002. Nitrate leaching as influenced by cover crops in large soil monoliths. Agron. J. 94, 807–814.
Luedeling, E., Zhang, M., Girvetz, E.H., 2009. Climate changes lead to declining winter chill for fruit and nut trees in California during 1950 – 2009. PLOS One 4, e6166. http://dx.doi.org/10.1371/journal.pone.0006166.
McKeown, A., Warland, J., McDonald, M.R., 2005. Long-term marketable yields of horticultural crops in southern Ontario in relation to seasonal climate. Can. J. Plant Sci. 85, 431–438.
Meehl, G.A., Stocker, T.F., Collins, W.D., Gaye, A.J., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, J.G., Weaver, A.J., Zhao, Z., 2007. Global Climate Projections. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Cambridge University Press, Cambridge, U.K. and New York, NY.
Peet, M., Sato, S., Clément, C.P., 2003. Heat stress increases sensitivity of pollen, fruit and seed production in tomatoes (*Lycopersicon Esculentum Mill.*) to non-optimal vapor pressure deficits. Acta Hort. (ISHS) 618, 209–215.
Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., 2006a. Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to high tissue temperature. Agric. For. Meteorol. (139), 237–251.
Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., Thomas., J.M.G., 2002. Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). Global Change Biol. 8, 710–721.
Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., Thomas, J.M.G., 2003. Supra-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L) reproductive processes and yield at ambient and elevated carbon dioxide. Global Change Biol. (9), 1775–1787.
Prasad, P.V.V., Craufurd, P.Q., Kakani, V.G., Wheeler, T.R., Boote, K.J., 2001. Influence of high temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in peanut. Aust. J. Plant Physiol. (28), 233–240.
Prasad, P.V.V., Boote, K.J., Allen Jr., L.H., Sheehy, J.E., Thomas, J.M.G., 2006b. Species, ecotype and cultivar differences in spikelet fertility and harvest index of rice in response to high temperature stress. Field Crops Res. (95), 398–411.
Prasad, P.V.V., Pisipati, S.R., Ristic, Z., Bukovnik, U., Fritz, A.K., 2008. Effect of nighttime temperature on physiology and growth of spring wheat. Crop. Sci. 48, 2372–2380.
Pressman, E., Peet, M.M., Pharr, D.M., 2002. The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers. Ann. Bot. 90, 631–636.
Reginato, G.H., Callejas, R.H., Sapiaín, R.A., García-de-Cortázar, V., 2010. Rest completion and growth of'thompson seedless' grapes as a function of temperatures. Acta Hortic. (ISHS) 872, 427–430.
Sacks, W.J., Kucharik, C.J., 2011. Crop management and phenology trends in the U.S. corn belt: Impacts on yields, evapotranspiration and energy balance. Agric. For. Meteor. 151, 882–894.
Satake, T., Yoshida, S., 1978. High temperature-induced sterility in *indica* rice at flowering. Jpn. J. Crop Sci. 47, 6–17.
Sato, S., 2006. The effects of moderately elevated temperature stress due to global warming on the yield and the male reproductive development of tomato (*Lycopersicon esculentum mill.*). HortResearch 60, 85–89.
Sato, S., Peet, M.M., Thomas, J.F., 2000. Physiological factors limit fruit set of tomato (*Lycopersicon esculentum Mill.*) under chronic, mild heat stress. Plant Cell Environ. 23, 719–726.
Schoper, J.B., Lambert, R.J., Vasilas, B.L., Westgate, M.E., 1987. Plant factors controlling seed set in maize. Plant Physiol. 83, 121–125.
Schlenker, W., Roberts, M.J., 2009. Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. Proc. Natl. Acad. Sci. 106, 15594–15598.
Seif, S., Gruppe, W., 1985. Chilling requirements of sweet cherries (*Prunus avium*) and interspecific cherry hybrids (*Prunus x ssp.*). Acta Hortic. (ISHS) 169, 289–294.
Sheehy, J.E., Elmido, A., Centeno, G., Pablico, P., 2005. Searching for new plants for climate change. J. Agric. Meterol. 60, 463–468.
Shah, F., Huang, J., Cui, K., Nie, L., Shah, T., Chen, C., Wang, K., 2011. Impact of high-temperature stress on rice plant and its traits related to tolerance. J. Agric. Sci 149, 545–556.
Singh, V., Nguyen, C.T., van Oosterom, E.J., Chapman, S.C., Jordan, D.R., Hammer, G. L., 2015. Sorghum genotypes differ in high temperature responses for seed set. Field Crops Res. 171, 32–40.
Sønsteby, A., Heide, O.M., 2008. Temperature responses, flowering and fruit yield of the June-bearing strawberry cultivars florence, frida and korona. Sci. Hortic. 119, 49–54.
Tesfaendrias, M.T., McDonald, M.R., Warland, J., 2010. Consistency of long-term marketable yield of carrot and onion cultivars in muck (organic) soil in relation to seasonal weather. Can. J. Plant Sci. 90, 755–765.
Timlin, D., Lutfor Rahman, S.M., Baker, J., Reddy, V.R., Fleisher, D., Quebedeaux, B., 2006. Whole plant photosynthesis, development, and carbon partitioning in potato as a function of temperature. Agron. J. 98, 1195–1203.
Wagstaffe, A., Battey, N.H., 2006. The optimum temperature for long-season cropping in the everbearing strawberry ´everest´. Acta Hortic. (ISHS) 708, 45–50.
Warrington, I.J., Fulton, T.A., Halligan, E.A., de Silva, H.N., 1999. Apple fruit growth and maturity are affected by early season temperatures. J. Am. Soc. Hortic. Sci. 124, 468–477.
Welch, J.R., Vincent, J.R., Auffhammer, M., Moya, P.F., Dobermann, A., Dawe, D., 2010. Rice yields in tropical/subtropical Asia exhibit large but opposing sensitivities to minimum and maximum temperatures. Proc. Natl. Acad. Sci. 107, 14562–14567.
Wiebbecke, C.F., Graham, M.A., Cianzio, S.R., Palmer, R.G., 2012. Day temperature influences the male-sterile locus *ms*9 in soybean. Crop Sci. 52, 1503–1510.