

crop iNIGHTS



High Night Temperature Effects on Corn Yield

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SUMMARY

- Corn producers are generally aware that high night temperatures can be detrimental to yield; however, the effects on specific plant processes and yield components are not as well understood.
- Corn originated in the Central Highlands of Mexico and adapted during its evolution to the predominant climatic conditions of this region, consisting of warm days and cool nights.
- Research has shown that above-average night temperatures during reproductive growth can reduce corn yield both through reduced kernel number and kernel weight.
- Current research supports two hypotheses that may explain why higher night temperatures during the grain filling period reduce grain yield.
 - The rate of respiration in the corn plant increases, requiring more sugar for energy, thus making less sugar available for deposition as starch in the kernel.
 - Higher temperature accelerates the phenological development of the corn plant, so the corn plant matures sooner.
- Although higher night temperatures undoubtedly increase the rate of respiration in corn, research generally suggests that accelerated phenological development is likely the primary mechanism affecting corn yield.

INTRODUCTION

Many agronomists and growers involved in corn production are aware of the idea that above-average night temperatures during pollination and grain fill can reduce corn grain yield. This concept is almost a “central dogma” in corn production. A summary review of the weather and corn grain yield data for 2009 and 2010 is just one of many examples that support this statement. In 2009, many farmers in the Midwestern United States produced record corn grain yields. However, in 2010, even with adequate rainfall, corn grain yields were much lower. A notable difference between these two growing seasons was night temperatures following pollination; in the states of Nebraska, Kansas, Iowa, Missouri, and Illinois, the average minimum night temperatures during July and August of 2009 were about 5–8°F lower than the average minimum night temperatures in 2010 (Figures 1 and 2).



Above-average night temperatures during pollination and grain fill can reduce corn grain yield.

Despite general awareness among corn producers that high night temperatures can be detrimental to yield, the effects on specific plant processes and yield components are not as well understood. The purpose of this *Crop Insights* article is to review some of the critical research literature relating corn growth and grain yield to temperature and to explore some of the mechanisms by which high night temperatures can affect grain yield.

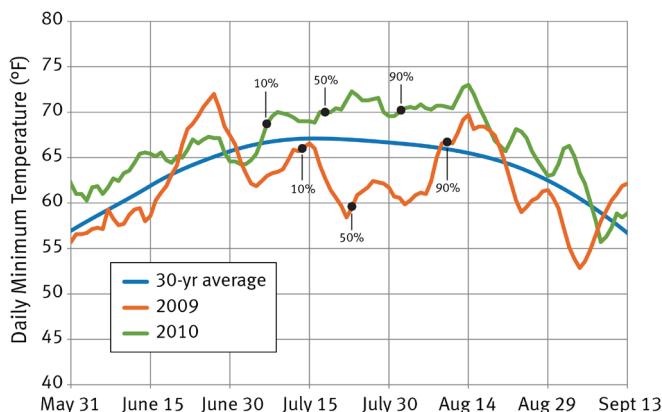
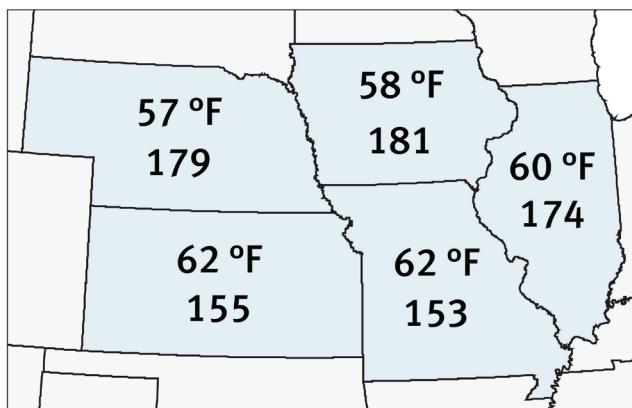


Figure 1. Daily minimum temperatures (7-day moving average) for Des Moines, IA, in 2009 and 2010, and 30-yr average minimum daily temperatures (1981-2010). Approximate dates of 10%, 50%, and 90% silking in Iowa in 2009 and 2010 based on USDA crop progress reports.

July-August 2009 Average Min. Temp. and Final Yield



July-August 2010 Average Min. Temp. and Final Yield

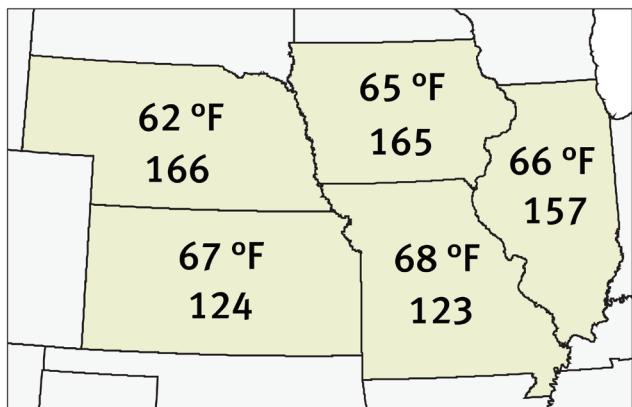


Figure 2. Average minimum temperatures experienced in July-August of 2009 (top) and 2010 (above) and average yields (bu/acre) in Iowa, Illinois, Missouri, Kansas and Nebraska. Data from NCEI NOAA, USDA NASS.

EXPERIMENTAL EVIDENCE OF NIGHT TEMPERATURE EFFECTS ON CORN YIELD

The first experimental evidence that high night temperatures can have a detrimental effect on corn yield came from an experiment performed by researchers at the University of Illinois (Peters et al., 1971). In this study, small climate-controlled enclosures were constructed and placed over corn plants at night to alter air temperature. Nighttime temperature treatments were imposed at flowering and maintained through physiological maturity. Corn grown with an average night temperature of 85°F yielded 40% less grain than corn grown with an average night temperature of 62°F (Table 1).

Although the impact on corn yield was substantial in this study, test results were not considered conclusive because the number of experimental test units was very small. Another concern about this study was a night temperature of 85°F is unrealistically high for the Central United States. Even with these concerns about the experimental design, this study triggered future research to explore how night temperatures affect grain yield and why the yield response occurs. In subsequent studies, researchers established that

higher night temperatures during reproductive growth can reduce corn yield both through reduced kernel number and reduced kernel weight.

Table 1. Effect of night temperature from silking through physiological maturity on corn yields (Peters et al., 1971).

Treatment	Average Night Temperature	Grain Yield
	°F	bu/acre
Natural Air	65	168
Cooled	62	162
Heated	85	100

A study by Cantarero et al. (1999) showed a reduction in kernel number associated with high night temperatures. This study examined the effects of elevated night temperature 9°F above ambient over a period extending from 1 week before silking to 3 weeks after silking. Results showed that kernel abortion in heated night plots was 8% higher than in the control plots. Ears in the heated plots had an average of 34 kernels per row at harvest, compared to 37 kernels per row in the control plots.

A study by Badu-Apraku et al. (1983) examined the effect of temperature on grain fill after kernel number had already been set. In this study, plants were grown in pots outdoors and then moved into controlled-temperature growth chambers 18 days after silking. Results showed that grain yield per plant was significantly affected by temperature regime (Table 2). The lowest temperature regime (77°F day, 59°F night) resulted in the greatest grain yield per plant as well as the longest grain fill duration. Increasing the night temperature to 77°F significantly reduced yield per plant. Increasing the day temperature to 95°F also resulted in lower yield per plant, regardless of night temperature.

Table 2. Effect of temperature on grain fill duration, grain weight per plant and kernel number (Badu-Apraku et al., 1983).

Day / Night Temperature	Grain Fill Duration*	Grain Wt Per Plant	Kernel Number
°F	days	oz	
77 / 59	39 a	4.4 a	550 a
77 / 77	31 b	3.6 b	580 a
95 / 59	24 c	2.5 c	593 a
95 / 77	21 d	2.4 c	606 a

* Interval from 18 days after silking to physiological maturity.

Values followed by the same letter are not significantly different at $\alpha = 0.05$.

THE RATE OF CORN GROWTH AND DEVELOPMENT IS RELATED TO ENVIRONMENTAL TEMPERATURE

Origins of Corn

When evaluating the effects of temperature on corn yield, it is important to consider the predominant conditions to which corn was adapted in its area of origin. Corn originates

from the Central Highlands of Mexico (Galinat, 1988). In this part of the world, the length of day changes little between the summer and winter months. Corn development does have some sensitivity to day length but the over-riding environmental factor affecting corn growth is temperature, primarily because temperature, rather than day length, is the more dominant environmental factor in central Mexico. The Highlands of central Mexico are similar to most of the highlands around the world. At higher elevations, day temperatures can be quite warm. However, night temperatures tend to be much cooler. During the evolutionary process, the corn plant adapted to grow best under warmer day temperatures and cooler night temperatures. The high-yielding hybrids of today still contain much of the genetic heritage of the corn plants that originally grew best in the high plains of Mexico.



Corn shocks in a field in central Mexico, the region where corn originated.

Development is Driven by Heat Unit Accumulation

Phenological development in corn is linked to the accumulation of heat units above a base threshold. For corn, the base level is 50°F and the upper threshold is 86°F. Growing degree unit (GDU) accumulation for a given day is calculated by the formula:

$$GDU = \left(\frac{\text{Daily Max Temp } ^\circ\text{F} + \text{Daily Min Temp } ^\circ\text{F}}{2} \right) - 50^\circ\text{F}$$

Higher temperatures increase GDU accumulation and increase the rate of thermal time that drives plant development. For example, a maximum temperature of 86°F and minimum temperature of 65°F results in a daily GDU accumulation of 25.5. However, a day with the same maximum temperature but a minimum temperature of 72°F results in a daily GDU accumulation of 29.

A General Concept Addressing the Physiology of Corn Growth

One way to better understand the physiology of corn growth is to compare corn physiology to that of human physiology. Humans are well-adapted for walking. For those of us who are in reasonably good health, it is relatively easy for us to walk a mile in about 15-20 minutes. However, if we decide to run a mile, this becomes more challenging. Our heart has

to beat at a higher rate, our lung capacity must increase, and our leg strength to endure the entire distance must improve. Our bodies must adjust to the increased demand for energy and muscle movement as we work and train to run a mile.

The corn plant originated from and has best adapted to growing in environments with warm days and cooler nights. As temperatures increase, the rates of physiological processes that support growth must also increase. If a person is running a mile, and this person loses energy, this person can stop and rest to allow all of the human physiological processes to slow down, such as “catching your breath”, slowing the heart rate down, and letting the muscles in your legs recover. The corn plant is fixed to grow in the location it is placed. Under these higher temperature environments, the physiological processes of the corn plant must keep going. However, at higher temperatures, the overall efficiencies of these processes decrease. The final outcome of this decreased efficiency from operating at a higher temperature is reduced grain yield.

CORN YIELD DETERMINATION

Corn grain yield production can be thought of as a two-step process. The first step is to establish the maximum potential yield or the maximum number of fertilized ovules that can be produced. The second step is to convert the maximum number of fertilized ovules to harvestable kernels. During all stages of the corn life cycle, meristematic cells are extracting all of the nutrients, water, and energy they can from the corn plant. These cells must be properly fed every day. If the corn plant faces a stress in which it cannot supply all of these necessary nutrients, water, and energy, some of these meristematic cells die. For grain yield, stress factors become particularly important during pollination when the meristematic cells are the ovules and young, fertilized embryos as well as during early grain fill when these young fertilized embryos are gaining size and weight. Approximately 85% of total grain yield is related to the total number of kernels produced per acre, and approximately 15% of the total grain yield is related to the weights of these kernels (Otegui et al., 1995).

The mechanism by which higher temperatures during pollination reduce the number of fertilized embryos per ear is not fully understood. Presently, there is evidence to support two hypotheses. For the first hypothesis, higher temperature is often associated with an increased potential for a water deficit or water stress to appear. There is a body of research that shows that water deficit in the developing ear during pollination limits the rate of silk growth. As silk growth slows, the ability for the pollen grain to form a pollen tube and fertilize the embryo in the developing ovule decreases, thus resulting in reduced kernel set (Oury et al., 2016a, 2016b). The second hypothesis is that the corn plant cannot produce and transport enough sugar to the developing ear. At higher temperatures, the corn plant is not as efficient in producing sugar. Embryos starting at the tip of the ear start to die due to starvation until the number of living embryos that remain can be adequately fed by the corn plant (Zinselmeier et al., 1995). Either one or some combination of both of these hypotheses could be correct.

If environmental conditions have been sufficient to produce a high number of fertilized ovules per ear, environmental conditions during grain fill dramatically affect the number of harvestable kernels per ear (Zinselmeier et al., 1995). Maximum kernel counts per ear have already been established. If stress occurs during this interval, the corn plant typically starts to abort kernels at the tip of the ear and moves toward the base of the ear until the number of remaining, viable kernels can be fed by the plant.

WHY DO HIGH NIGHT TEMPERATURES REDUCE YIELD?

Current research supports two hypotheses that may explain why higher temperatures during the grain filling period reduce grain yield. The first hypothesis is that the rate of respiration in the corn plant increases as the temperature increases. Increased respiration requires more sugar for energy, thus making less sugar available for deposition as starch in the kernel. The second hypothesis proposes that higher temperature accelerates the phenological development of the corn plant, so the corn plant matures sooner. This faster growth rate forces the physiological processes to run more quickly and less efficiently, thus reducing grain yield. Research evidence to support each of these hypotheses follows.

Higher Rate of Respiration

The most commonly cited explanation for the detrimental effect of high night temperatures on corn yield is increased expenditure of energy due to a higher rate of cellular respiration at night. This concept is illustrated in Figure 3, which compares plant dry weight accumulation between warmer and cooler night temperature conditions, assuming equivalent temperatures during the day.

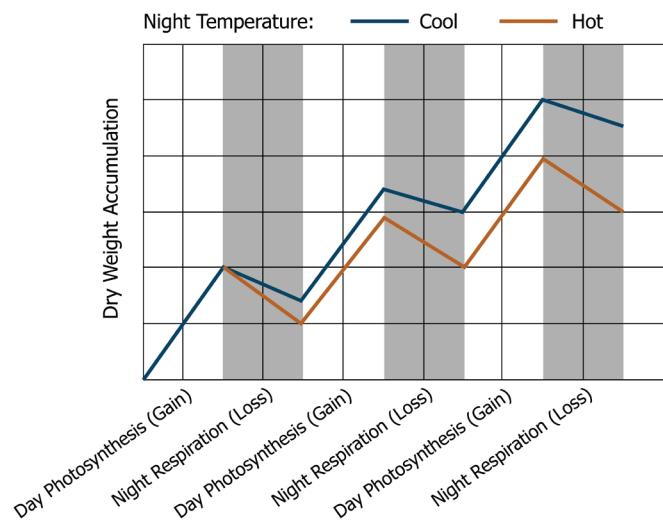


Figure 3. Dry weight accumulation related to night temperature. Growth involves accumulation of dry weight from photosynthesis during the day and loss from respiration at night. (Adapted from Hoeft, et al., 2000)

Higher temperatures produce faster rates of cellular respiration in a corn plant. Cellular respiration consumes carbon assimilated through photosynthesis (sugar) to obtain the energy necessary to maintain and increase plant biomass.

Respiration can be subdivided into growth respiration and maintenance respiration. Growth respiration is the expenditure of carbon that contributes to the growth of the plant. Maintenance respiration provides energy to processes that do not directly contribute to an increase in plant biomass or plant weight. The two are distinguished based on the relative growth rate of the plant; at a zero growth rate, all respiration contributes to maintenance. The proportion of respiration contributing to plant growth tends to be greater in younger developing tissues, whereas respiration in mature tissues is mostly for plant maintenance. Maintenance respiration also tends to be greater in the roots than in the aboveground portions of the plant.

Respiration provides the energy necessary to drive critical plant processes, but respiration can also consume carbon (sugar) with little or no yield of useful energy to the plant. A lower rate of respiration (sugar consumption) relative to photosynthesis (sugar production) has generally been viewed as favorable for maximizing agricultural productivity and grain yield. Temperature-dependent biological reactions, such as photosynthesis and respiration, generally have an optimum temperature (T_{opt}) for operation (Figure 4).

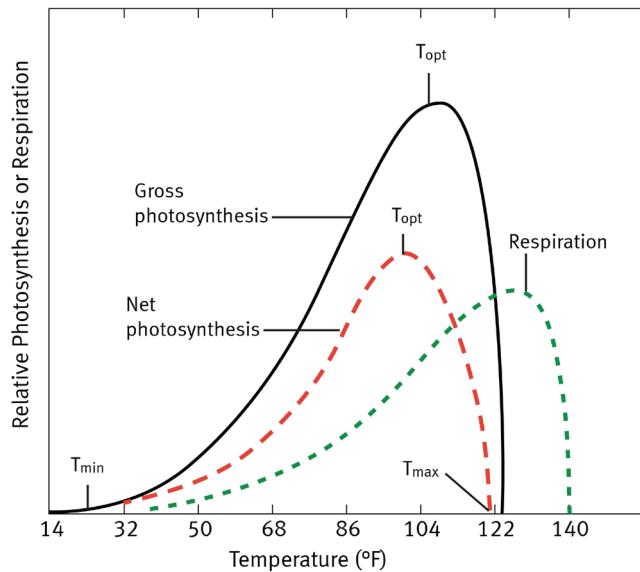
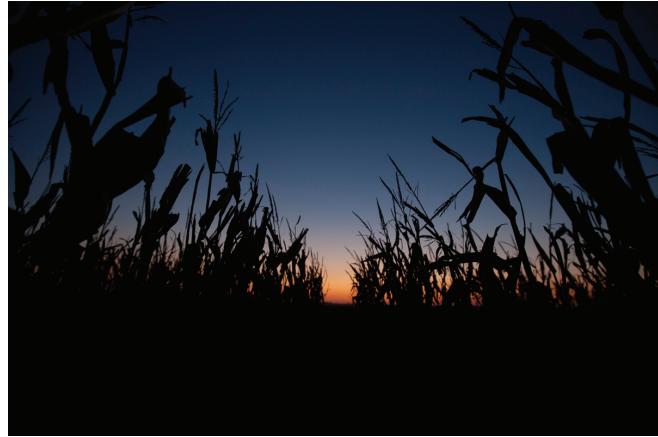


Figure 4. Temperature effects on rates of gross photosynthesis, respiration, and net photosynthesis. (Adapted from Hopkins, 1999)

Photosynthesis and respiration are slow at cooler temperatures, increase as the temperature increases, and cease when the temperature gets too high. The optimum temperature for respiration is greater than that for photosynthesis. Net photosynthesis is a measure of carbon assimilated through photosynthesis (sugar produced) minus carbon expended through respiration (sugar consumed) and has a T_{opt} lower than that of gross photosynthesis. Grain yield is more closely associated with the rate of net photosynthesis (the red line in Figure 4). Optimum corn growth occurs at about 86°F. Note in Figure 4, the optimum temperature for photosynthesis in corn is about 100°F. The discrepancy in temperature is because the temperature on the upper surface of a corn leaf on a bright sunny day is a few

degrees higher than the surrounding air temperature. We measure the air temperature, but the chloroplasts where photosynthesis occurs in the corn leaf respond to the leaf temperature. From a grain yield perspective, if the daytime temperature remains the same and the nighttime temperature increases, respiration during the night increases. The end result is that net photosynthesis (the red line in Figure 4) decreases, and less sugar is available for conversion to starch that is deposited in the kernel.



Accelerated Phenological Development

The second hypothesis for why high night temperatures reduce corn yields is accelerated phenological development resulting in a shorter grain fill period. The researchers who conducted the yield study presented in Table 1 noted that the elevated night temperature reduced the time required for corn plants to reach physiological maturity. This observation triggered substantial research to study how the rate of corn development during grain fill affects grain yield. Shortening the length of time between silk emergence and maturity reduces the number of days that the corn plant is engaged in photosynthesis during grain fill, effectively reducing the amount of energy the corn plant can convert into grain yield. Based on long-term average daily minimum and maximum temperatures for Des Moines, IA, a 111 CRM hybrid that reaches 50% silk on July 10 is physiologically mature on September 2. A 2-week period following silking during which night temperatures are 5°F above normal shortens the time to maturity by 2 days.

Following the 2010 growing season, in which lower than expected crop yields were attributed to above-average night temperatures following silking, Iowa State University researchers used the Hybrid-Maize model to explore the effects of night temperature on length of grain fill (Elmore, 2010). The model was used to compare predicted days to physiological maturity for corn at five Iowa locations based on actual 2010 temperatures vs. the same temperature regimes with the daily minimum temperatures from July 15 to Aug 15, replaced with those from the 2009 growing season (labeled as T_{min} Alt in Table 3). Daily minimum temperatures during this period averaged around 8°F cooler in 2009 than 2010 in Iowa. Results of these simulations showed that lower night temperatures during the month-long period following silking extended grain fill by a week or more for all five of the locations.

Table 3. Simulations conducted with Hybrid-Maize resulting days in reproductive stages and total days to maturity in five Iowa State University Research and Demonstration Farms.

ISU Research Farm	Year	Days in Reproductive Stages	Total Days to Maturity
Sutherland	2010	61	131
Sutherland	2010 T_{min} Alt	72	144
Nashua	2010	55	122
Nashua	2010 T_{min} Alt	63	130
Ames	2010	50	115
Ames	2010 T_{min} Alt	59	124
Lewis	2010	50	115
Lewis	2010 T_{min} Alt	58	123
Crawfordsville	2010	50	114
Crawfordsville	2010 T_{min} Alt	57	120

Data from Elmore, 2010. For each location, the days calculated for the T_{min} Alt value are based on minimum temperatures extracted from the 2009 growing season.

Research conducted by Badu-Apraku et al. (1983) provides further evidence that shortening the days from silk emergence to physiological maturity reduces grain yield. Results showed that duration of the grain fill period and grain yield per plant were both significantly affected by temperature regime (Table 2). The lowest temperature regime (77°F day, 59°F night) resulted in the longest grain fill duration and produced the greatest grain yield per plant. The increased night temperature of 77°F significantly reduced grain fill duration and yield per plant. Increasing the day temperature to 95°F also resulted in shorter grain fill duration and lower yield per plant, regardless of night temperature. These results show that higher temperatures overall, either during the day or during the night, accelerate phenological development, shorten the grain fill period, and reduce kernel weight.

Presently, the preferred hypothesis is that higher temperatures during grain fill shorten the reproductive period during grain fill, thus reducing final grain yield.

Although higher night temperatures undoubtedly increase the rate of respiration in corn, research generally suggests that higher rates of night respiration probably do not have a substantial impact on corn yield. In a study that examined the effects of elevated night temperature over a period extending from one week before silking to three weeks after silking, night respiration in plant leaves did not significantly differ between the heated and control plots (Cantarero et al., 1999). This may be because corn is a C-4 plant that has a biochemical pathway to capture carbon dioxide that may be respired during the night until the next day when this carbon dioxide can be consumed during photosynthesis.

In another study that measured both leaf and whole plant respiration in corn, respiration rates were found to be high for newly emerged plants but declined as plants developed (Quin, 1981). These researchers concluded that increased respiration rates associated with high night temperatures likely did not have a major impact on corn yield. Research on other crop species has produced similar findings. The carbon flux associated with photosynthesis typically far exceeds that associated with respiration, so changes in respiration rate due to higher night temperatures have a relatively small effect on net photosynthesis (Frantz et al., 2004).

The majority of the research generally shows that accelerated phenological development is likely the primary mechanism by which high night temperatures can negatively affect corn yield. Faster plant development reduces the total amount of photosynthesis carried out by the plant during reproductive growth. In addition, photosynthesis per unit of thermal time during the critical period following silking decreases. Consequently, high night temperatures can affect both kernel number and kernel weight depending on timing and duration of heat stress.



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