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A REVIEW :

Effect of heat stress on pulse production

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Pooja Goswami, Pratibha Bisen and Richa Singh

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Author for correspondence :

Pooja Goswami Department of Agronomy, College of Agriculture (JNKVV), Balaghat (M.P.) India Email: agropooja17@ gmail.com

See end of the article for authors' affiliations

India is largest producer of pulses in the world with 25 per cent share in global production. Majority of the pulse-growing regions are vulnerable to climate change as maximum threshold temperature for tolerance of pulses has already been reached beyond 35°C. Chickpea, pigeonpea, mungbean, uradbean, lentil and fieldpea are important pulses crop contributing 39 per cent, 21 per cent, 11 per cent, 10 per cent, 7 per cent and 5 per cent to the total production of pulses in the country. The total production was estimated 14.56 million tonnes and an area of 23.63 million hectares with average productivity 625 kg/ha. Climate change will surely have an adverse impact on productivity on account of reduction of total crop cycle duration. Most of the pulses like mungbean and uradbean short duration crop.

The impact of heat stress on pulse production:

Heat stress often is defined as where temperatures are hot enough for sufficient time that they cause irreversible damage to plant function or development. In addition, high temperatures can increase the rate of reproductive development, which shortens the time for photosynthesis to contribute to fruit or seed production. I also will consider this as a heat-stress effect even though it may not cause permanent (irreversible) damage to development because the acceleration does substantially reduce total fruit or grain yield.

Among the pulses, pigeonpea is very sensitive to abrupt fluctuations of temperatures either lower or higher extremes leading to massive flower drop.

The negative impact of temperature extremities is largely compensated by regular fresh flush of flower that keep on appearing during the developmental stages as and when the temperature is favourable. However, at extreme high temperature the serious adverse impact was observed on pod setting.

For cool season pulse crops daily maximum temperature above 25°C is considered as threshold level for heat stress, as it affects seed yield by reducing flowering, fertilization and seed formation.

Cool season pulses such as chickpea, lentil lathyrus have reasonably high tolerance to wheat which enables them to set pod but filling of pods is seriously jeopardized at high temperature leading low productivity.

Fieldpea is highly sensitive to heat at bloom. A brief exposure to high temperature during flowering cause heavy loss due to flower dropt and pod abortion and during filling. It can reduce seed set weight and accelerate senescence, resulting reduce the seed yield.

The extent to which heat stress occurs in specific climatic zones is a complex issue. Plants can be damaged in different ways by either high day or high night temperatures and by either high air or high soil temperatures. Also, crop species and cultivars differ in their sensitivity to high temperatures. Cool-season annual species are more sensitive to hot weather than warmseason annuals. In Table 1 there are several examples of cool-season and warm-season annual crop species. I did not include safflower in the table because it is unusual in that during the vegetative stage it grows well in cool conditions and during the reproductive stage it grows well in hot conditions.

Table 1: Annual crop species adapted to cool and warm seasons (Hall, 2001)	
Cool-season annuals	Warm-season annuals
Barley, brassicas, canola, fava bean, flax, garbanzo bean, Irish potato, lentil, lettuce, lupine, mustard, oat, pea, radish, rye, spinach, triticale, turnip, vetch, wheat	Common bean, cotton, cowpea, cucurbits, finger millet, grain amaranth, lima bean, maize, mung bean, pearl millet, pepper, pigeonpea, rice sesame, sorghum, soybean, sunflower, sweet potato, tobacco, tomato

High day temperatures can have direct damaging effects associated with hot tissue temperatures or indirect effects associated with the plant-water-deficits that can arise due to high evaporative demands. Evaporative demand exhibits near exponential increases with increases in day-time temperatures and can result in high transpiration rates and low plant water potentials (Hall, 2001).

The extent of heat stress that can occur in a specific climatic zone depends on the probability of high temperatures occurring and their duration during the day or night. Where global climate change is occurring these probabilities may not be predicted well based only on historical records for specific locations. Heat stress is a complex function of intensity (temperature degrees), duration and rate of increase in temperature. The magnitude of heat stress rapidly increases as temperature increases above a threshold level and complex acclimation effects can occur that depend on temperature and other environmental factors.

High soil temperatures can reduce plant emergence. The maximum threshold temperatures for germination and emergence are higher for warm-season than for coolseason annuals. For example, the threshold maximum seed zone temperature for emergence of cowpea is about 37°C compared with 25 to 33°C for lettuce.

During the vegetative stage, high day temperatures can cause damage to components of leaf photosynthesis, reducing carbon dioxide assimilation rates compared with environments having more optimal temperatures. Sensitivity of photosynthesis to heat mainly may be due to damage to components of photosystem II located in the thylakoid membranes of the chloroplast and membrane properties (Al-Khatib and Paulsen, 1999). Membrane thermostability has been evaluated by measuring electrolyte leakage from leaf disks subjected to extreme temperatures (Blum, 1988). More stable membranes exhibit slower electrolyte leakage. Studies comparing responses to heat of contrasting species indicated that photosystem II of the cool season species, wheat, is more sensitive to heat than photosystem II of rice and pearl millet, which are warm season species adapted to much higher temperatures (Al-Khatib and Paulsen, 1999).

Extreme temperatures can cause premature death of plants. Among the cool-season annuals, pea is very sensitive to high day temperatures with death of the plant occurring when air temperatures exceed about 35°C for sufficient duration, whereas barley is very heat tolerant, especially during grain filling. For warm season annuals, cowpea can produce substantial biomass when growing in one of the hottest crop production environments on earth (maximum day-time air temperatures in a weather station shelter of about 50°C), although its vegetative development may exhibit abnormalities such as leaf fasciations. For monocotyledons, including both coolseason and warm-season annuals, high daytime temperatures can cause leaf firing which involves necrosis of the leaf tips and this symptom also can be caused by drought.

Reproductive development of many crop species is damaged by heat such that they produce no flowers or if they produce flowers they may set no fruit or seeds. Discuss the detrimental effects of heat stress on reproductive development that has been reported for cowpea, common bean, tomato, cotton, rice, wheat, maize and sorghum. I will examine the detrimental effects of heat stress on cowpea because of the comprehensive

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information available for this species and the likelihood that many of the same phenomena occur with other warm-season crop species.

Controlled-environment studies in which cowpea plants were subjected to separately controlled root and shoot and day and night temperatures demonstrated that pod set (the proportion of flowers producing pods) was damaged by moderately high night temperature of the shoot (Warrag and Hall, 1984a and b). It was surprising that night temperature would have this effect since much hotter day temperatures did not damage pod set of cowpea. Reciprocal artificial pollinations between plants grown under high and optimal night temperatures indicated the low pod set was caused by male sterility and that the pistils did not appear to be damaged by high night temperature. The detrimental effects of high night temperature on pod set also were shown to occur in field conditions (Nielsen and Hall, 1985b). In these experiments a unique experimental approach was used in which plots of cowpea plants were subjected to different increments of higher night temperatures during early stages of flowering using enclosure systems placed over the plots only during the night-time (Nielsen and Hall, 1985a).

Possible mechanisms for the sensitivity of pod set to high night temperatures have been proposed. Mutters and Hall (1992) demonstrated that there is a distinct period during the 24-hour cycle when pollen development in cowpea is sensitive to high night temperatures. Plants subjected to high temperature during the last six hours of the night exhibited substantially decreased pollen viability and pod set, whereas plants subjected to high temperature during the first six hours of a twelve-hour night exhibited no damage. Mutters and Hall (1992) hypothesized that these results could be explained if a heat-sensitive process in pollen development is under circadian control and only occurs in the late night period. Note that if a heat-sensitive process is under circadian control and if genetic variation exists for the time in the 24-hour cycle when this process occurs, evolution in hot environments would favor plants in which the heatsensitive process occurs at the coolest time which is just prior to dawn. The damaging effect of high night temperature on pod set was greater in long days than in short days, and red and far red light treatments indicated it is a phytochrome-mediated response (Mutters et al., 1989b).

Studies were conducted in which cowpeas were

transferred between growth chambers having high or optimal night temperatures (Warrag and Hall 1984b and Ahmed *et al.*, 1992). They demonstrated that the stage of floral development most sensitive to high night temperature occurs 9 to 7 days prior to anthesis, which is after meiosis and coincides with release of pollen microspores from the tetrads. Damage due to high night temperature was associated with premature degeneration of the tapetal layer that provides nutrients to developing pollen, infertile pollen and in some genotypes anthers did not dehiscence. The transfer of proline from the tapetal layer to pollen was inhibited (Mutters *et al.*, 1989a).

Comparisons of heat-sensitive and heat-tolerant cowpeas showed a genotypic association between sensitivity to heat during pod set and rapid leakage of electrolytes from leaf discs subjected to heat stress (Ismail *et al.*, 1999). Possibly, the damage to pollen development by high night temperatures may be in some way associated with a heat-induced malfunction in membrane properties.

Floral bud development also can be damaged by heat such that plants do not produce flowers. For cowpea, two weeks or more of consecutive or interrupted hot nights during the first month after germination caused complete suppression of floral bud development (Ahmed and Hall, 1993). In extreme cases the floral buds become necrotic and die. In field conditions, the damage occurs under long days but not under short days. However, responses to red and far red light indicated the effect was only partially consistent with the system being mediated by phytochrome (Mutter et al., 1989b). The damaging effect of high night temperature and long days on floral bud development also depended on light quality whereas the damaging effect on pod set did not depend on light quality (Ahmed et al., 1993b). When growth chambers were used with relatively large amounts of fluorescent light and little incandescent light, such that the red/far red ratio was 1.9, floral buds were not suppressed in long-day high night temperature conditions, but pod set was very low. This artificial light system provides a useful experimental method for studying the effects of heat stress on pod set without complications due to heat stress effects on floral bud development. When growth chambers were used with lighting systems providing a red/far red ratio of 1.3 to 1.6, floral bud suppression was observed that was similar to what is obtained under long-day high night temperature conditions in the field where sunlight has a red/far red ratio of about



1.2.

Pods of different cowpea genotypes produce 9 to 20 ovules with many cultivars having 15 ovules, but pods rarely produce these many seeds per pod. Under optimal conditions two-thirds of the ovules may produce seed, whereas with high day or high night temperature (Warrag and Hall, 1983) and other stresses, such as drought, fewer seeds are produced per pod. For most cultivars and stresses it is the ovules at the blossom end of the pod that suffer embryo abortion and do not produce seed, resulting in the production of "pinched" pods.

Cowpea seeds produced under high day temperatures can have asymmetrical twisted cotyledon. Germination of the seed is not influenced and this effect of heat stress may not be a major problem for commercial production. In contrast, heat-induced brown discoloration of cowpea seed coats can occur with some cultivars and be a major problem causing consumers to reject grain. Higher night temperatures resulted in progressively larger numbers of seed with larger areas of brown discoloration on seed coats (Nielsen and Hall, 1985b).

The extent to which high-temperature damage to photosynthesis or reproductive development affect fruit or grain yield probably depends on the extent to which the photosynthetic source and the reproductive sink are limiting fruit or grain yield and this may vary among species and cultivars.

Surface and internal tissues of tomato and citrus fruit can be damaged by the combination of high temperatures and intense solar radiation. High tissue temperatures also can damage cambium layers in exposed trunks and branches

More rapid pod development may increase the extent of embryo abortion, and individual seed usually are smaller in tropical compared with subtropical conditions for the same cowpea cultivar. Pulsess subjected to elevated night-temperature treatments produced smaller seed. The more rapid development of individual fruits also results in the overall reproductive period of the plant being shorter. Grain yields of cowpea cultivars grown with optimal management are much less in tropical zones than in subtropical zones mainly due to the shorter overall reproductive period caused by the hot nights of tropical zones. Acceleration of reproductive development also is a problem for cool season crops, such as wheat, growing in environments that are hot during reproductive development Direct evidence for heat-stress effects on grain yield was provided by the studies of Nielsen and

Hall (1985b) in which cowpea was subjected to different increments of elevated night temperature under field conditions in a subtropical location in California. For minimum night temperatures greater than 15°C there were linear reductions in both grain yield and the proportion of flowers that set pods with 50 per cent reductions occurring at minimum night temperatures of about 26°C.

Authors' affiliations :

Pratibha Bisen and Richa Singh, College of Agriculture, Balaghat (M.P.) India

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