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Impact of Elevated Temperature and Carbon dioxide on Seed Physiology and Yield

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Abstract

Food security is of utmost priority to humankind. This is the implication of various interconnected factors that lead to climate change. Elevated temperature and carbon dioxide levels are just two of these. The nutrient is an inseparable aspect of food. The change in climate is posing threat not only to the amount of available food but also to the nutrients laden in the food items. Seeds are the miniature form of plants and are a reflection of their future health and nutritional status. The changes in environmental factors predominantly challenge the growth and development of a seed. This review is an attempt to understand the impact of elevated CO_2 and temperature on seed germination, the nutritional status of the seed and the yield in form of total seed production. It gives a direction for analysis and future studies that may use the latest available tools like gene editing to tackle and counteract the retarding effect of climate change on these parameters of seed, thereby offering a climate resilient agriculture.

Keywords

Climate change, elevated CO_2, heat stress, seed germination, yield

Introduction

Seeds represent a significant stage in the life cycle of a plant and are vital component in maintaining the continuous exixtence of a species. They store the genetic information required for the next generation to disperse, establish, develop and reproduce. The seed is a fascinating organ as it has the capability to maintain life in a hidden form if present in a dry state (dormancy) and to recommence its metabolic activities during favorable environmental conditions. The climatic factors are important determinants and play a key role in affecting the various stages in the life cycle of a plant starting from the germination of seed till its development (1).

The global temperature of the earth's surface may increase by 2.5-4.5^{0}C, due to anthropogenic activities, resulting in the release of carbon dioxide gas and the emission of other greenhouse gases (2). As a consequence, plant species distribution and vegetation structure in near future can be drastically altered and it could also adversely affect the existence of the individual species. The effects of temperature on plant growth and development are the source for predicting germination timing. The factors which affect seed germination are temperature, soil moisture, light intensity, seed size and seasonal variation. All these factors whether single or in combination can influence the germination % and rate (3). Among all factors that affect germination, the temperature is the major limiting factor (4, 5). Exposure to high temperatures during seed development for a long duration delays germination and reduces the seed vigor and dry mass (6) directly impacting the plant growth and development. Elevated temperature can enhance the rates of photorespiration and transpiration and therefore reduces the rate of photosynthesis, affecting the growth of seedling establishment and development (7).

Each individual species has an optimum temperature, below and above these temperatures, germination cannot occur. The three important parameters regarding the temperature which strongly influence seed germination are moisture, hormonal and enzymatic activity. For germination, seeds need to imbibe water and thus sufficient moisture should be present. Hot and dry climate conditions enhance evaporation and reduce moisture, which could negatively impact seed germination. Besides physical factors, plant hormones like gibberellins and abscisic acid (ABA) also regulate seed germination. Seed germination is enhanced by the gibberellins and on the other hand, Abscisic acid inhibits seed germination and promotes dormancy. Genes that control the production of these hormones, enzymes that facilitates the elongation of embryo and radicle protrusion and other chemical signaling pathways are also dependent on temperature (8). An extreme change in temperature could negatively impact and may have some serious implications also on seed germination. Similarly, elevated carbon dioxide (eCO_2) results in carbon fertilization effects but it also hampers the overall growth and development of most species.

There are not many studies on seed germination under the influence of elevated temperature and eCO_2. Information on seed dormancy, yield, viability and % germination is vital for the growth and survival of any plant species. Therefore, this paper aims to bring a basic but deeper understanding of the effect of these factors on various aspects of seed development, seed germination, nutrient content and yield. This understanding may be helpful in devising an appropriate scientific solution to mitigate climate change-induced damage to crops and plants in general.

Impact on Seed germination

The agricultural productivity of most crops is heavily dependent on the post-zygotic reproductive product, most often which is the seed. Though the post-zygotic output is directly related to the pre-zygotic stages for an agriculture-based economy of the world, the focus is generally the quantity and quality of the seed, which will not only feed its populations but also set rolling the next cycle for the species. Seeds of cereals form the major source of food globally. Therefore, the impact of high temperatures on their seed size, weight, and nutrient content is another very important parameter that needs the attention of scientists. Heat stress (39^{0}C) modified the initiation of cellularization of endosperm in rice during the post-zygotic phase (1 d after fertilization), which led to altered biosynthesis pathway gene expression in gibberellic acid and abscisic acid (ABA) and reduction in the seed size and starch content (9).

A study conducted on seed germination in rice showed a reduction from 100 % to 60% when the temperature was increased from 37 to 50^{0}C for 96 hr period. The same temperature for the same time period was given to maize and sorghum also, where the germination was reduced by up to 40%. When exposed to the high temperature, the seedlings of all three crops, showed signs of stagnation (10). In peanuts (*Arachis hypogea* L.), temperatures greater than 40±1^{0}C, the occurrence of deformed seedlings was noticed and the temperature beyond 50^{0}C had a harmful effect on seeds in the form of embryonic death (11). An endemic tree species of China, *Pinus bungeana* Zucc. ex Endl., showed the maximum seed germination (90%) at 15 or 20^{0}C with or without light, whereas at 25-30^{0}C, there was a reduction in the seed germination as well as the emergence of the radicle was also delayed (12). Similar studies conducted on *Pinus densiflora*, *P. thunbergii* and *Maackia amurensis* showed that high temperature not only reduced percent germination but also delay it, representing that seed germination of *Pinus* species is highly sensitive to high temperature (13, 14).

In carrots, the optimal germination occurs between 20^{0}C to 30^{0}C (15) and like other crops, abiotic stress also reduced the yield in carrots (16, 17), as well as the high temperature, inhibited the seed germination in carrots (18). In *Arabidopsis*, complete seed germination was reported at 22^{0}C, whereas the seed exposed at 34^{0}C suppressed germination by 90%, resulting that heat stress having an adverse impact on seed germination (19, 20).

Reduction in the seedling and their survival percentage was observed in *Crassocephalum crepidioides*, where it decreased linearly as the duration of the heat treatment was increased and approximately all the seeds were killed after 6-days of heating at 40^{0}C (21).

On the contrary, in some plant species, the high temperature increased the germination percentage as high temperature can activate the chemical pathways leading to seed germination. The lower mean germination time of *Corylopsis gotoana* var. *coreana* and *Prunus padus* seeds with impervious hard seed coats were more prominent at the elevated temperature (8, 22). Similarly, in black gram, the highest seed germination (93%) was observed when the seeds were treated at 50^{0}C for 20 min, followed by the seeds exposed for 10 min (88%), indicating that high-temperature treatment increased the seed germination. Heat exposure for a longer duration (30 min.) inhibited seed germination to 80%, but this germination percentage was higher than the control seeds which were not given any kind of heat stress (23).

Carbon dioxide has also been shown to enhance the germination percentage of seeds of various plants at relatively high concentrations (24). In *Amaranthus hybridus*, *Chenopodium album* and *Medicago sativa*, doubling the concentration of CO_2 increased the germination % (25). On the contrary, another study conducted on *Malus baccata*, *Picea jezoensis* and *Zelkova serrata* demonstrated that seed germination was significantly lower under elevated CO_2 concentration indicating that increase in CO_2 concentration always do not have a beneficial effect on seed germination (20, 26).

Impact on Seed yield

Industrialization, deforestation and large-scale agriculture, the emission of greenhouse gases into the atmosphere have risen to a record level, resulting in increased temperature. Various investigations undoubtedly confirm that high temperatures will have strong negative implications on the agriculture sector soon, particularly in some emerging economies.

Research has also shown that seed yields of canola have been reduced by 15% by subjecting the crop to high-temperature stress before flowering (27). The effects of elevated CO_2 and temperature on the productivity of three main cropping systems in Punjab were investigated. Results indicated that on doubling the level of CO_2 (350 ppm) at the existing temperature, yields of paddy in rice, seed-cotton in cotton and grain in maize, were increased by 4.9, 5.5 and 6.5% respectively (28). Several other studies have observed the effect of elevated CO_2 levels on the nodule size, nodule number and biomass/seed yield in legumes like *Pisum sativum*, *Trifolium repens*, *Lupinus albus*, soybean and common bean and noted an increase in these parameters (29-32). They reasoned that the improvement was due to greater N_2 fixation under elevated CO_2 (33).

Contrary to the eCO_2 effects, higher-than-required temperatures bring down crop yields. The yield was substantially lowered with an increase in the maximum and minimum optimal temperatures of maize, rice and cotton. The percent decrease in wheat equivalent yield in various cropping systems was 2, 23 and 39 with maximum and 12, 11 and 17 with minimum temperature respectively (28).

Temperature affects the different growth parameters, yield and quality in soybean too. This crop is susceptible to variations in temperature. The ambient temperature range for this crop is 15-22^{0}C at emergence, 20-25^{0}C at flowering and 15-22^{0}C at maturity (34). The yield of soybean seed improved between 18/12^{0}C (day/night) and 26/20^{0}C, but the yield was reduced at temperatures higher than 26/20^{0}C (35, 36). Temperature rise from 29/20 to 34/20^{0}C at the seed fill stage lowered the seed yield (37) and temperature above than 40^{0}C severely limited the pod formation (38). In soybean, a higher incidence of abnormal seedlings was also revealed, when the seed was exposed to a temperature greater than 28^{0}C (39). In Phaseolus, Vulgaris highest seed yield occurred at 28/18^{0}C, but as the temperature increased, yield started declining, at 37/27^{0}C, the yield was zero (40). In wheat, the reduced yield was observed in terms of decreased chlorophyll content, photosynthesis and transpiration rate (41).

Higher temperature also adversely impacts the translocation of photosynthates (42) to the developing seeds thereby reducing the seed weight and number (yield) and altered metabolism may reduce the seed germination (43). Faster seed filling was held responsible for small-wrinkled seeds in lentils (44) and chickpeas (45). The higher CO_2 affects whole-plant development rate mostly indicated by the time to reach the reproductive phase. Different plants respond differently to the changing environment by either slowing (46), or fastening (47, 48) the development processes. Species may exhibit slower, or similar rates of development in response to elevated CO_2 (48). The ones showing faster development acquired a minimum size necessary for the reproduction or changed the size at which plants begin reproduction (49). By preponing the time of reproduction, the plant-pollinator interaction is affected (48) and reduces the final seed production or yield.

Impact on Seed Quality

High temperature affects some physiological and biochemical processes like oxygen requirement during seed imbibitions (50). In *Arabidopsis*, it was reported that the accumulation of ABA and reactive oxygen species are increased due to the high temperature, resulting in the dormancy of seeds and thus limiting seed germination (51). Heat shock proteins (HSPs) are produced because of heat stress and are linked to dormancy (52). These HSPs retain the proteins in the seed in a folding-competent mode which restricts germination until the occurrence of favorable conditions (53).

HSPs can weaken some of the physiological processes linked with seed size and quality. These heat shock proteins reduced the levels of sugars such as fructose, sugar nucleotides and hexose phosphate as well as significantly decreased the starch accumulation during grain filling in wheat (54), rice (55) and maize (56). The decrease in the level of sugars may be linked to assimilate utilization for purposes other than edible component production (57).

In soybean and in cereals, increased temperature and CO_2 enrichment reduced protein and micronutrient content (58, 59). Under heat stress, the nutritional value of total free amino acids and total protein concentration was reduced in soybean, whereas the oil concentration was considerably increased (60). A decrease in nutritional (mainly N, Zn, Fe and S) quality was reported in non-legume C3 crops (61), *Lactuca sativa*, *Spinacia oleracea* (62), faba bean and lentil (63) under increased CO_2 concentrations. A decreased amount of nitrogen, phosphorus and potassium was also observed in the edible parts of both *L. sativa* and *S. oleracea* (62). Elevated CO_2 concentration hampers the quality of crops by reducing the nutrients like minerals, proteins and vitamins (64). It is speculated that the low nutrients will result in the loss of quality of cereals, pulses and other food plants and are a threat to ecosystem sustainability and food security.

Effects on parameters other than seed

Heat shock proteins (HSPs) not only affect the quality and content of the seed but also have undesirable impacts on the plant growth, yield as well as it also affects the physiological processes of the plants such as reduction in the photosynthetic rate and increased respiration rate (65). These HSPs have negative effects on root development, (66) and reproductive stages including the developmental stages of the flowering and pollination process (67).

Cotton (*Gossypium hirsutum*) flowers when exposed to high temperature, showed lowered ATP production as well as reduced carbohydrate reserves (particularly sucrose) in their pistils, associated with a heat stress-induced reduction in the rate of photosynthesis (68). It was suggested that a stress-induced reduction in sugar delivery to reproductive tissue led to the failure of gametophyte development (69). A significant decline in the number of soluble carbohydrates and ATP content in the pistil of cotton was observed when the plant was exposed (38^{0}C/20^{0}C) for a week before flowering, resulting in a reduction in the number of ovules and fertilization efficiency (68).

Similarly, it was observed that sugar starvation is the major cause of the failure of fertilization in rice when the plants were exposed to elevated temperatures (70). It can be linked with the presence of acid invertase enzymes as invertase hydrolyze sucrose into hexose and thus provides carbohydrates from transmitting tissue to support pollen tube growth (71, 72). Under heat stress, the activity of the invertase enzyme was significantly decreased and thus restricting the supply of hexose sugars. The interaction between sugars and hormones is indicated in sugar transport (73, 74) whereas other scientists have reviewed the carbon dynamics and suggested not to draw a general conclusion about the role of sugars in crop reproduction (75). Providing the exogenous acid invertase increased the amount of carbohydrates content as well as increased the spikelet fertility in rice (76). In maize, the grain size and yield were reduced at 30^{0}C due to problems in endosperm cell division and replication of amyloplast (77). Counteracting climate change needs a holistic approach so that the effects on the reproductive phase of plants can be minimized (78) and the abiotic threats to biodiversity can be addressed (79).

Conclusion and future perspective

Due to global climate change, these environmental cues are getting altered and it may enhance, delay or inhibit germination percentage, as has been observed in some cases. Predicted changes in temperature, precipitation and soil moisture, are going to affect several aspects of seeds such as seed longevity, dormancy, germination and soil pathogen activity. An increase in temperature may change the overall species distribution by affecting seed germination, growth and fitness, thereby having incredible ecological as well as economic consequences (80). Therefore, it has become necessary to thoroughly evaluate the outcomes of temperature and carbon-di-oxide on individual species and ecosystems as a whole to tackle the drastic situation of climate change. Developing thermotolerant species using genetic and molecular tools. This calls for a thorough grasp of the responses of plants to changing temperatures and the mechanism(s) of heat tolerance to devise possible strategies for improving crop thermotolerance.

Further studies should be directed to understand the combined effect of various environmental factors such as elevated CO_2 concentration and higher temperatures. eCO_2 results in enhanced growth and biomass of plants on one side it is too early to predict the impact on carbohydrate and hormone signaling may have. The complex interaction of biotic and abiotic factors needs to be investigated at the molecular level to come up with a better understanding of thermotolerance and carbon sequestration. Genetic engineering is a very promising approach to genetically engineering biotic and abiotic stress-tolerant and resistant species, but it has not been able to deliver its potential due to strict regulations and public perception and concerns about GM products. Various approaches such as mathematical modeling based on various crop growth attributes can be used to predict the yield and manage appropriate resources in time (81, 82). Transcriptional reprogramming using recent techniques like gene editing may be another tool that may be utilized to understand the plant responses to the changing environment and equip humanity to counteract or at least minimize its impact and pave way for much acceptable solution to climate-resilient agriculture.

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Authors contributions

All authors contributed equally in conceptualising the study, manuscript preparation, revision and approval of the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

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