Influence of maternal temperatures on seed quality: (review)

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Abstract

Temperature is one of the most important environmental factors affecting not only plant growth and development leading to low yield potential of crops, but also the quality characteristics of the progeny and the seed. The influence of temperature on vegetative growth and reproductive yield components has been extensively studied, but less is known about the effects of temperature during seed growth, development and maturation on seed quality in terms of germination and vigour. Evidence from the existing literature shows that parental growth temperatures strongly influence the quality of the seed produced.

This paper reviews these studies and examines the effect of parental temperatures on different components of seed quality (physical, physiological and biochemical) and the possible mechanisms of parental temperatures inducing these changes on seed germination and vigour.

Key words: Temperature, germination, vigour, seed

Résumé

Influence de la température maternelle sur la qualité de semences (Revue bibliographique)

La température est un des principaux facteurs environnementaux affectant non seulement la croissance et le développement des plantes et limitant la productivité potentielle des cultures, mais aussi a une grande influence sur la qualité de la progeniture des plantes, la semence. L'influence des températures sur la croissance végétative et reproductive des plantes a été largement étudiée. Cependant, peu est connu sur l'effet des températures au cours du développement et de la maturité des grains, sur la germination et la vigueur des semences.

Les études antérieures ont pu montrer que les températures de croissance maternelle jouent un rôle important dans la détermination de la qualité de semence produite. Cet article résume les différentes études et analyse l'effet des températures au cours de la production de semence sur les différentes composantes de la qualité de semences (physique, physiologique et biochimique), ainsi que les mécanismes possibles qui peuvent induire ces changements au niveau de la germination et de la vigueur de semence.

Mots-clés: température, germination, vigueur, semences

ملخص : تأثير الحرارة على جودة البذور

كراس ل.
المركز الجهوي للبحث الزراعي، سطات، المغرب

تعتبر الحرارة أهم العوامل البيئية التي تؤثر ليس فقط على نمو النبات و قدرتها الإنتاجية، بل لها كذلك تأثير كبير على جودة البذور (الإنبات و قدرة الإنبات). إن تأثير الحرارة على نمو النباتات كان موضوع دراسات عديدة، و لكن تأثير الحرارة خلال نمو و نضج البذور على الإنبات و قوته لم يحظ بنفس الاهتمام و تظل المعلومات حول هذا الموضوع محدودة. أظهرت الدراسات السابقة أن الحرارة خلال نمو النبات "الأم" تلعب دورا مهما في تحديد جودة البذور. هذا المقال يلخص مختلف الدراسات حول هذا الموضوع و يحلل مدى تأثير الحرارة خلال إنتاج البذور على مختلف مقاييس جودتها (فيزيائية، فيزيولوجية و بيوكيماوية) و يعطي إضافة لهذا نظرة على "الميكانيزمات" التي بإمكانها أن تخلق هاته التغيرات على مستوى انبات و قوة إنبات البذور.

كلمات مفتاحية : الحرارة، الإنبات، قوة الإنبات، البذور.

Introduction

Most cultivated crops start from seeds. Therefore, having high seed quality is important both for the producer and the user. Seeds, in their lifetime, are exposed to three different environments (Harman and Stasz 1986): the seed production field environment, where seeds form, develop and mature; the storage environment, where seeds are conditioned and kept until needed; and the soil environment, where seeds are put in the soil to regenerate new plants. To produce and preserve a high quality seed, optimum conditions should be maintained at each level. Because this is unlikely to occur, decreases in seed quality are inevitable. Deterioration may take place either during the development and the maturation of the seed on the mother plant or while the seed is in storage (Helm *et al.* 1989). It has been reported that vigour and viability differences arise as early as during seed development (Dell'Aqiula and Toritto 1991).

It is well known that the germination and viability of seeds may vary greatly from year to year and from one production site to another. Much of this variation has been attributed to the environmental conditions prevalent during the formation, development and maturation when the seed is still attached to the mother plant. Different studies have shown that extensive damage to developing and maturing seeds can be caused by different types of environmental stress such as freezing, high temperature, inadequate water supply and mineral deficiencies (Austin 1972; Delouche 1980; Dornbos *et al.* 1989; Frey 1981; and Tekrony 1981). Mild climatic conditions during the pre harvest period usually contribute to high quality seed, whereas adverse conditions often result in rapid losses of viability and vigour of the mature seed (Delouche 1980).

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Depending on the stage of development, high temperatures may strongly influence the quality of the mature seed. For the purpose of this review we divided seed quality into three major categories: physical (seed size, seed mass, and seed chemical composition), physiological (seed dormancy, seed germination, and seed vigour), and biochemical (respiratory system, nucleotide pools, and proteins and nucleic acids synthesis). This review examines these three quality categories changes which may take place as a result of heat stress while the seed is still attached to the mother plant, and the probable mechanisms of heat stress on seed quality.

Physical seed quality

It is well established that temperature has a major influence on the final grain yield in cereals. The response, however, varies with the stage of development. High temperatures during booting stage or before anthesis greatly reduce grain number per ear (Wardlaw *et al.* 1989). Tashiro and Wardlaw (1990a) reported that seed set adjustments mostly occur within 10 days after anthesis. An increase in temperature from 21 to 30 °C immediately following anthesis resulted in a decrease in seed number. After the seed number has been determined, cereal grain yield becomes proportional to kernel weight which is function of the rate and duration of grain filling period (Wiegnand and Cuellar 1981). High temperatures during or following anthesis adversely affect both these parameters (Wardlaw *et al.* 1980). Field and growth chamber experiments confirm that heat stress, at this period of seed development, enhances initial grain growth rate but shortens the grain filling period (Bauer *et al.* 1985; Bruckner and Frohberg 1987; and Sofield *et al.* 1977). However, such compensation occurs only under mild stress (15 to 21 °C) and not under severe stress (21 °C and above). Under the latter conditions the decrease in the duration of the grain filling period is no longer balanced by an increase in the grain growth rate (Bhullar and Jeuner 1983; Sofield *et al.* 1977; and Wardlaw *et al.* 1980). As a consequence, the mature seed mass at higher temperatures is much reduced.

Heat stress may also alter other physical seed traits while it is still on the mother plant. The specific type and extent of damage depends on the time of the stress treatment in relation to the stage of grain development. Tashiro and Wardlaw (1990b) reported a wide range of grain damage when they applied high temperature treatments during the period from head emergence to the early stages of seed development. High temperatures, two to three days before anthesis, resulted in a high frequency of sterile grains. Parthenocarpic, abortive, shrunken, split, notched and opaque grains were induced by high temperatures during and after anthesis. The same authors, Tashiro and Wardlaw (1990ab), reported that heat stress strongly influenced wheat grain dimensions. Grain length at maturity was mostly sensitive to high temperatures applied seven days after anthesis while grain width was most sensitive at 12 - 21 days after anthesis. Similar results have been reported in beans by Abdussidique and Goodwin (1980). They noted a high frequency of irregularities in the final appearance of the seeds subjected to high temperatures immediately after pod set. Khan and Laude (1969) had observed that the thickness of barley grain seed coat decreases with longer exposure of the developing seed to high temperatures. Keigley and Mullen (1986) found that the high temperature environment during soybean seed filling period increased the percentage of small, etched and discolored seeds, and reduced the seed weight.

Seed chemical composition also may vary with the stage of development and the prevailing environmental conditions. Bewley and Black (1985) described the time course of carbohydrates, lipids, and protein composition changes during the development of cereal seeds. Starch and proteins are the major constituents of a mature wheat seed. Their content and proportion per grain is determined by the interaction of the genotype with the environment. The increase in protein content of the seed is positively correlated with environmental stresses such as high temperatures and inadequate water supply (Bhullar and Jeuner 1985; and Spiertz 1977). In general, this increase is mostly due to a reduction in the starch content of the grain and not to a change in the quantity of nitrogen.

Physiological seed quality

The physiological quality of the seed has also been reported to be influenced by parent seed environment (Fenner 1991). Differences in seed dormancy may be genetic in origin but, are also influenced by the environmental conditions during seed development and ripening (Hagemann and Ciha 1987; and Sawhney and Naylor 1978). It is well established that the degree and extent of post-harvest seed dormancy are strongly affected by the combination of the environmental conditions under which seed had developed and matured. With some exceptions, a decrease in seed dormancy is positively correlated with high temperatures during seed maturation (Fenner 1991). Koller (1962) showed that warm temperatures during the maturation of lettuce seeds reduced dormancy. Similarly, Gray *et al.* (1988) reported that high temperatures alleviate or prevent the occurrence of dormancy in lettuce. This reduction in dormancy by higher temperatures during seed development has also been demonstrated in the wild oats (Sexsmith 1969), barley (Khan and Laude 1969) and wheat (Reddy *et al.* 1985). Several studies have reported that high temperatures at the time of seed development and ripening shortens the dormancy period of wheat seeds (Olsson and Mattsson 1975; and Lalluka 1976). For these species that exhibit post-harvest dormancy, high temperatures during seed development often result in higher germination percentages due to a decrease in seed dormancy. As a general rule, high temperatures during seed development and maturity favor a decrease in seed dormancy. The exceptions to this general observation are those species which express little or no post-harvest seed dormancy. In this case high parent growth temperatures result in a decrease in germination and/or vigour of mature seed. Keigley and Mullen (1986) reported that high temperatures during soybean seed fill reduced germination and vigour of mature seeds. High temperature stress during corn seed maturation also affected subsequent seedling emergence and reduced seedling vigour as indicated by root and shoot dry weight (Frey 1981). Fussell and Pearson (1980) found that the temperature during which the pearl millet grain was developed did not affect seed viability. However, grains developed at low temperatures produced more vigorous seedlings than those developed at high temperatures. Mohamed *et al.* (1985) found that the high temperature conditions during millet seed development affected seed size, and subsequently, germination rate and seed viability. Similarly, Steiner and Opoku-Boateng (1991) demonstrated that high air temperature (daily maximum >35 °C) shortly before and after anthesis reduced vigour of mature lettuce seed. Similar results have been reported for crisp lettuce seeds (Gray *et al.*, 1988). Datta *et al.* (1972) reported that temperature regime under which the mother plants grew affected germination speed and germination percentage of the Aegilops caryopses. In their study on oat, Sawhney and Quick (1985) demonstrated that even the temperatures during vegetative growth (up to anthesis) can influence the germination behavior of the resulting seeds. Walter and Jensen (1970) reported that air and soil moisture regimes during alfalfa seed production not only affected seed yield, size and germination but also influenced vigour of subsequent seedlings. Moss and Mullett (1982) demonstrated that seed vigour in beans can be modified by varying the temperature during seed production over several generations. However, negative response, an increase in temperature during seed development has been reported to increase seed germination and vigour in some species, such as barley (Khan and Laude 1969), bracted plantain (Stearns 1960), onions (Gray and Steckel 1984) and sugar beet (Wood *et al.* 1980).

From the literature cited above, evidence exists that temperature during seed development and maturation can affect seed germination. The general pattern which has emerged from most of these studies is that a large proportion of the variation in seed germination was explained either through a seed size and/or seed dormancy and little has been done about seed vigour properties.

Reduction in seed size due to heat stress during reproductive growth is commonly reported for many species as a result of altered seed growth rates and seed filling durations. Also, positive correlation between seed weight, seed germination and seedling vigour were reported by Datta *et al.* (1972) in agilops species, by Dornbos and Mullen (1991) in soybean grown under high temperatures and water stress, by Steiner and Opoku-Boateng (1991) in lettuce seeds, and by Walter and Jensen (1970) in alfalfa seeds. Other studies reported changes in seed size under high maternal temperatures but not associated with changes in seed quality as in cotton (Quisenberry and Gipson 1974) and *Plantago aristata* (Stearns 1960). So, the question which remains unclear is whether these changes in seed size alone can explain the detrimental effects of heat stress seen in germination and seed vigour. Abdussidique and Goodwin (1980) reported that this effect can still be seen even when the high temperatures were imposed later in maturation of soybean, after seed size had been determined. This may suggest that in addition to the reduction in seed size, heat stress may cause some metabolic changes leading to reduced seed germination and vigour. In plants, it is well known that most metabolic reactions such as protein synthesis, photosynthesis and membrane integrity are affected by high temperatures (Harding *et al.* 1990; Raison *et al.* 1980). However, in seeds this kind of information is still lacking. Similar studies are needed to investigate the effects of temperatures during seed production on seed metabolic reactions.

Seed dormancy is the most intensively studied phenomenon as far as temperature is considered. For most agricultural species, dormancy is positively correlated with temperature. High temperature conditions during seed production lead to reduction in seed dormancy and consequently to high seed germination. However, this effect could be seen only for seeds that are tested immediately after harvest. In order to study the actual effect of temperature on seed germination and vigour, this confounding between seed germination and dormancy should be eliminated. This can be done either by allowing ample time for the seed to overcome dormancy or by alleviating the dormancy before any seed testing. On the other hand, seed germination alone does not provide sufficient performance information on the seed. Seed lots which show high germinability in the laboratory may demonstrate poor field emergence. A more sensitive measure of seed quality is provided by seed vigour tests. Thus, studies should be oriented to the understanding of the effect of high temperatures on seed vigour instead of seed germination. Recent study by Grass (1994) indicated that high temperatures during seed development and maturation had no effect on wheat "Oum-rabia" seed germination but reduced seed vigour.

Biochemical seed quality

Physiological differences in seed performance are usually dependent on the biochemical metabolism of the seed during its early stages of imbibition. One of the apparent biochemical changes that occurs at this stage of the germination process is an increase in oxygen uptake. It is well known that respiration is necessary for growth. Its relationship with seed germination has been suggested to be based on two important roles: it provides the required energy to the germinating seed and it reflects both the integrity and the overall activity of the metabolic machinery of the seed (Dell'Aquila and Toritto 1991). Beevers and Hanson (1964) found that both respiration and phosphorylation, in corn seedling roots and shoots, were affected by high temperatures. Also, Madden (1992) reported that high temperature treatment during seed desiccation resulted in mitochondria damage of maize seed axes. Similar results have been reported by Grass (1994) for wheat seeds. Exposing wheat seed, during its development and maturation, to high temperatures resulted in low oxygen consumption by seed embryos and low mitochondria activity. Seed deterioration during storage, or accelerated ageing, may also result in a delay in mitochondria activation, a decrease in respiration rates and respiratory control ratio values, and a lower phosphorylative efficiency (Fergusson *et al.* 1990; and Woodstock *et al.* 1984).

Seed germination is a biological process that requires energy. This energy in the form of nucleotides plays a major role in germinating seed metabolism; it participates and regulates all phases of carbohydrates, lipids, proteins and nucleic acids metabolism (Mangat 1982). Adenosine triphosphate (ATP) is regarded as the main form of the available energy. However, dry seeds do not accumulate any ATP. Therefore, their production at the early stages of seed imbibition is essential for successful germination and in directing the growth and developmental processes that occur during seed germinating (Moreland *et al.* 1974; and Perl 1986). Different environmental stresses were shown to influence the ATP level and/or the adenylate energy charge (AEC). Mangat (1982) reported that a combination of high air and soil temperatures resulted in low levels of total free nucleotides, nucleotide triphosphate, ribonucleic acid (RNA), and protein in soybean seedlings. Similar metabolic changes occur during other environmental stressful conditions. Turner and Wellburn (1985) showed that the ATP levels in leaves of sweet pepper were very sensitive to water stress, where a small change in leaf water potential resulted in significant reduction in leaf ATP content to 70-80 % of the control. Mendelssohn and McKee (1985) reported that nutrient stress resulted in greatly reduced adenylate pools in marsh plant leaves. Ching (1982) stated that any chemical or herbicide treatment that inhibits respiration, photosynthesis, or growth tends to reduce ATP content in seeds and young seedlings. Madden (1992) showed that desiccation temperature over 40 °C resulted in a reduction of all the high energy nucleotide levels during the early stages of maize seed germination. Recent study by Grass (1994) revealed a decrease both in the nucleotide content and the adenylate energy charge of wheat embryos excised from seeds grown under high temperature conditions. Several investigators have also reported that ATP levels increase slowly during the hydration of aged seeds (Ching 1973; Ching and Danielson 1972; Lunn and Madsen 1981).

Deterioration of seed quality may take place either during seed development and maturation on the mother plant or while the seed is in storage. The rate of deterioration is dependent upon the environmental conditions to which the seed is exposed to. The first quality component to show deterioration is that of seed vigour, followed by germination and finally seed death (Spears 1995). The assessment of seed vigour is based on the physical, physiological and biochemical performance of the seed. These physiological and biochemical processes are generally the first detectable changes that occur during the deterioration of the seed quality. So, changes in seed metabolism machinery may take place before it is even possible to detect any decrease in viability as measured by the conventional germination test. In other words, germination loss is the last phenomenon that takes place in any seed quality deterioration. Respiratory metabolism of germinating seeds, especially mitochondria activity, loss of energy (ATP) during the initial stages of seed germination, membrane integrity as measured by seed conductivity are all measurable components that contribute to the assessment of seed vigour. Recent research has made little progress in this direction in pointing out mitochondria as the primary target of heat stress (Madden 1992; Grass 1994) but we are still far from proposing the mechanism of heat stress operating during seed development which controls germ inability and seed vigour. Further investigation is still needed in this area.

Mechanisms of heat stress on seed quality

Many hypotheses have been suggested regarding the mechanisms of heat injury to cultivated plants. These hypotheses have been ranked by Levitt (1972) as direct or indirect heat injuries. Direct heat injury involves both lipid and protein change which results in membrane damage. Loss of membrane integrity at high temperatures could be due either to excessive fluidity and phase transition of lipids or to denaturation and aggregation of membrane proteins. Indirect heat injury involves primarily damage of major organelles such as mitochondria and chloroplasts. In seeds, the precise mechanism of heat stress, during seed development, and its effects on physiological and biochemical metabolism of the resulting mature seed is still unknown. However, a number of theoretical processes have been formulated regarding seed deterioration either in the field or in storage. One of the extensively studied mechanisms is membrane integrity and its chemical composition. Halmer and Bewley (1984) in their review of seed vigour, suggested membrane integrity as an important determinant factor of seed vigour. Excess solute leakage from seeds often indicates reducea vigour (Association of official seed analysts 1983). Basvarajappa *et al.* (1991) provided evidence for the loss of membrane integrity as the probable first deteriorative change during ageing in maize seeds. Several studies have reported that environmental stress during seed growth, development and/or maturity strongly alter the chemical composition of the seed membranes. Dornbos *et al.* (1989) have shown that drought stress and high temperature during seed fill strongly influenced the fatty acid composition of membrane phospholipids in soybean seeds. Dornbos (1988) in his review of the effect of high parent growth temperature on seed phospholipid composition concluded that membrane lipid composition and fluidity may represent one of the mechanisms of heat injury on seed quality.

Recent studies on seed quality suggest possible influence of temperature on the mitochondria activity and structure of seed embryo during its early stages of germination. Madden (1992) found that high temperature desiccation resulted in a reduced mitochondria activity of maize embryos. These changes were accompanied by a noticeable decrease both of nucleotide content and AEC values of maize embryos, and consequent low seedling vigour. Similar results have been reported by Grass (1994) where high temperature during seed development and maturation had negatively influenced the respiratory metabolism of wheat embryos and resulted in low seedling vigour. This impairment of mitochondria was also associated with a decrease in the available energy (ATP) during early germination. The author (Grass, 1994) suggests that mitochondria may be one of the probable targets of heat stress injury to seed.

Other hypotheses of heat injury to seed quality may involve alteration in the expression of one or several components of seed metabolism such as enzymatic machinery, gene expression, desiccation tolerance, and heat shock proteins. Bewley and Marcus (1990) reported that the expression of some genes that regulate developmental processes can be altered by environmental factors during seed development. Heat stress is known to induce synthesis of heat shock proteins (HSPs). Abernethy *et al.* (1989) suggested that these HSPs could be synthesised as a normal part of seed development and retained during seed desiccation; or they may be synthesised only in response to high temperature stress during seed maturation. Howarth (1990) reported that long-lived RNAs in the dry seed, including mRNAs encoding for HSPs, can be synthesised during seed-ripening period. The author (Howarth 1990) suggested that the environmental conditions prevalent during development and maturation of the seed modify the subsequent thermosensitivity during germination. In other words, these environmental conditions may affect the ability for the synthesis of HSPs in the early stages of germination. Helm *et al.* (1989), in their study on wheat embryos, concluded that low vigour embryos do not synthesise as much of HSPs as normally synthesised by high vigour embryos. The same authors suggested that this decrease in HSPs response is due to specific lesions in the gene expression in low vigour seeds.

Conclusion

In any seed multiplication program, a knowledge of how environmental conditions affect seed yield and quality is of considerable importance in producing high-quality seeds. This could be of practical importance to the seed's man in choosing cultivars and the site of seed production. Temperature is one of the important factors that influences not only plant growth and development (yield), but also the quality of its progeny the seed .

It is evident from the literature that temperature strongly influences seed quality. The effects of this abiotic stress vary widely among species and varieties and the response depends on the time and the exposure period to high temperature. Depending on the crop cycle, heat stress influences the physical parameters of seed quality, in particular seed size and seed appearance. Physiological criteria of seed quality are strongly affected by heat stress. In highly dormant species, caution is warranted in distinguishing the dormancy factor from changes in the inherent physiological quality of the seed in response to maternal growth temperatures. Since any change on the physiological quality must be related to changes in the biochemical metabolism of the seed, it seems that any effects of temperature during seed development on seed germination and vigour would be mediated through a physiological or biochemical origin.

Review of the literature reveals that the temperature-induced changes in seed quality suggest that maternal growth temperatures play an important role in seed quality determination.

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