https://doi.org/10.1590/1678-4499.20230297

BASIC AREAS
Article

Evaluation of biochemical component determinants for superior seedling performance in high-vigor maize seeds under accelerated aging stress

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Received: Dec. 22, 2023 | **Accepted:** June 17, 2024

Section Editor: Hector Valenzuela

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How to cite: Silva, M. B. P., Coelho, C. M. M. and Siega, Y. P. (2024). Evaluation of biochemical component determinants for superior seedling performance in high-vigor maize seeds under accelerated aging stress. Bragantia, 83, e20230297. https://doi.org/10.1590/1678-4499.20230297

ABSTRACT: Under stressful conditions, the use of high-vigor seeds is a relevant alternative to reduce losses, as they can germinate in a wide range of environmental conditions. However, it is necessary to understand the biochemical strategies adopted by high-vigor seeds to achieve better performance during periods of stress. Thus, the objectives of this research were to evaluate the tolerance of maize seeds of contrasting vigor subjected to different levels of stress due to accelerated aging and to verify whether differences in antioxidant metabolism and starch reduction explain the differences between vigor levels. The experiment was conducted with a high-vigor seed lot and a low-vigor seed lot, in a completely randomized design. The lots were subjected to 0, 24, 48, 60 and 72 hours of accelerated aging (45°C and 100% relative humidity), and after that the tests were carried out. The variables analyzed were the percentage of normal (first and second count) and abnormal seedlings, dead seeds, vigor index, electrical conductivity, total soluble sugars in the leachate, alpha-amylase activity, soluble sugar content, catalase activity, peroxide hydrogen, lipid peroxidation, proline, and carotenoid content. High-vigor seeds better tolerate stress conditions caused by high temperature and humidity. The higher content of total soluble sugars and alpha-amylase activity may explain the better performance of high-vigor seeds.

Key words: antioxidant metabolism, seed physiology, sugar metabolism, *Zea mays*.

INTRODUCTION

From physiological maturity to the emergence of seedlings in the field, seeds are susceptible to adverse environmental conditions, mainly regarding to temperature and humidity. The effect of these conditions is negative for seedling performance, with reductions in germination speed and uniformity (Marcos-Filho 2015). In these situations, the vigor of the seeds is decisive for overcoming stress and establishing the plant stand (Reis et al. 2022), as vigor represents the potential of a seed lot to quickly produce normal and uniform seedlings under a wide range of environmental conditions (Marcos-Filho 2015).

Vigor is highly inversely correlated with the state of seed deterioration, as it consists of degenerative physiological and biochemical changes that occur in the seed from physiological maturity. The speed at which these degenerative processes occur varies depending on the initial quality of the seed and the environmental conditions (Navarro et al. 2015).

Vigor tests precisely identify the state of deterioration of a seed lot, as is the case of accelerated aging, which subjects the seed to deterioration due to high temperature and relative humidity and evaluates its germination after this process (Kryzanowski et al. 2020). Thus, accelerated aging can be also used to identify physiological and biochemical differences between lots of contrasting vigor levels throughout deterioration.

Deterioration shows harmful effects on maize seeds (Timóteo and Marcos-Filho 2013, Marcos-Filho 2015). Understanding the physiological, metabolic, and biochemical differences that occur during this process in lots of different vigor levels

helps in identifying biochemical markers for greater vigor. These markers can be used as quick tests to detect vigor levels in breeding programs, as biochemical analyses are relatively quick (Andrade et al. 2020). The greater tolerance of high-vigor seeds to stress is associated with biochemical overcoming mechanisms, such as increased production of enzymes and antioxidant substances (Prazeres et al. 2021) and increased degradation of starch and availability of sugars for embryo growth and damage repair (Nerling et al. 2018).

In this context, the hypotheses of this study were: high-vigor seeds have greater tolerance to different levels of stress, managing to produce better performing seedlings; and the differences found in the metabolism of seeds of contrasting vigor subjected to stress explain the better performance of seedlings originating from seeds of high vigor. Therefore, the objectives of this research were to evaluate the tolerance of maize seeds of contrasting vigor subjected to different levels of stress due to accelerated aging and to verify whether differences in antioxidant metabolism and starch reduction explain the differences between vigor levels.

METHODS

This study was carried out in the Seed Laboratory of the Department of Agronomy of the Universidade do Estado de Santa Catarina in the municipality of Lages, SC, Brazil. The experiments were performed using hybrid maize commercial seeds from the cultivar DKB 230 PRO3 produced in the harvest of 2021/2021. This cultivar is widely grown in Santa Catarina state, and the sample used in this study was donated by the producer company. This work was divided into two experiments: selection of high- and low-vigor seeds; and evaluations in response to seed aging treatment (Fig. 1).

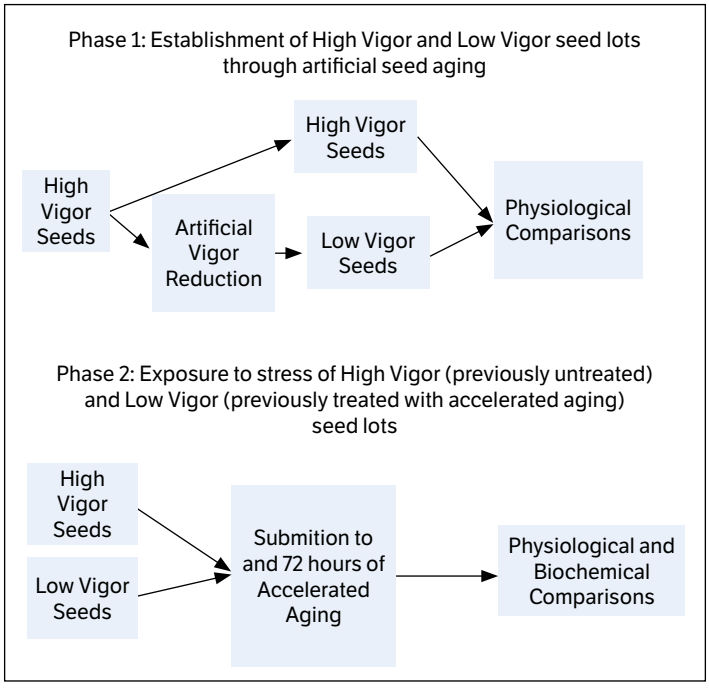


Figure 1. Sequence of the experimental protocol to establish high- and low-vigor seed lots, and their subsequent exposure to accelerated aging.

Establishment of high- and low-vigor seed lots through artificial seed aging

To obtain contrasting vigor seed lots for subsequent tests, half the seeds was subjected to artificial reduction of vigor through accelerated aging (Kryzanowski et al. 2020). The procedure was carried out in polystyrene boxes with 40 mL of distilled water at the bottom, on top of metal screens. The boxes with the seeds were taken to the accelerated aging chamber,

in which they remained for 36 hours at a temperature of 45 ± 2°C and 95% relative humidity (RH). At the end of this period, the seeds were placed in an air circulation oven at 30°C for 12 hours to reduce their moisture percentage to 13%. The artificially aged seeds were used as low-vigor seeds, and unaged seeds were used as the high-vigor seeds.

To verify the effect of artificially reducing vigor, four replications of each lot were evaluated based on germination (first and second counts), accelerated aging and vigor index. The design used in this phase was completely randomized, and analysis of variance and Tukey's mean comparison test were performed ($p < 0.05$) with Sisvar statistic software. The tests were conducted as described ahead.

Germination tests were carried with four replications of 100 seeds for each lot, which were placed on paper rolls moistened with distilled water at 2.5 times their weight. The rolls were placed in germination chambers at 25°C, and germination was assessed four (first count) and seven days (total germination) after sowing (DAS), according to the rules for seed analysis (Brasil 2009).

For accelerated aging test, four replications of 50 seeds were placed on metal screens inside gerbox-type plastic boxes with distilled water at the bottom, and then subjected to a temperature of 45°C for 72 hours in an accelerated aging chamber. After this period, the seeds were transferred to previously moistened germitest paper rolls and subjected to a germination test with evaluation at 4 DAS (Kryzanowski et al. 2020).

The vigor index was adapted from Kryzanowski et al. (2020) with four replications of 20 seeds. The seeds were placed to germinate on previously moistened paper rolls and placed in germination chambers at 25°C for three days. After this period, the length of the shoot and root was measured. With these values, the vigor index was calculated, according to the combination of formulas (Eq. 1):

$$\text{Vigor} = ([(SL \times 10) + (RL \times 90)] \times 0{,}7) + [1000 - (0.75 \times sSL + 0.5 \times sRL + 2.5 \times stotal + 50 \times sRLSL) - 0 \times ndead] \times 0{,}3) \quad (1)$$

where: SL: the average length of the shoot; RL: the average length of the root; sSL: the standard deviation of the shoot; sRL: the standard deviation of the root; stotal: the standard deviation of the seedling; sRLSL: the standard deviation of the root/shoot ratio; ndead: the number of dead seeds.

Exposure to stress of high- (previously untreated) and low-vigor (previously treated with accelerated aging) seed lots

To estimate the tolerance of the seed lots to different levels of stress, they were subjected to accelerated aging (45°C at 95% RH), with a methodology similar to that presented previously, but with different periods (24, 48, 60 and 72 hours) of stress. Control treatments were unaged and preconditioned seeds from both high- and low-vigor seeds. After these periods, the following physiological tests were carried out.

The assessment of normal and abnormal seedlings and dead seeds was carried out with four replications of 50 seeds per treatment, arranged on previously moistened germitest paper rolls. The paper rolls were placed in Mangelsdorf-type germination chambers at 25°C. The evaluations were carried out at four and seven DAS based on the criteria of the seed analysis rules (Brasil 2009), and results expressed in percentage.

Accelerated aging was applied using the methodology by Kryzanowski et al. (2020), as previously indicated.

For electrical conductivity, as described by Kryzanowski et al. (2020), four replications of 50 seeds per treatment were used. First, the seeds were weighed and placed in plastic cups along with 75 mL of distilled water. Two glasses with only water (blank) were also used to make white corrections. The cups were placed in a germination chamber at 25°C, in which they remained for 24 hours. After 24 hours, the electrical conductivity of the solution was measured using a conductivity meter. Values are expressed in $\mu S \cdot cm^{-1} \cdot g^{-1}$ of seed.

The results of the tests were compared with analysis of variance, and the means of the seed lots were compared using the Tukey's test ($p < 0.05$) and Sisvar statistic software. Regression analysis was performed to characterize the behavior of variables according to the periods of stress.

Biochemical analysis

Aiming to verify the relation between some biochemical components from sugar and oxidative metabolism and seed performance under stress conditions, the following evaluations were carried out in four replications of 20 seeds per treatment. These biochemical components are known to have a potential role in seed vigor and the seed's response to stress. The two seed lots went through 0, 24, 48, 60 and 72 hours of stress due to accelerated aging, and then the seeds were frozen in liquid nitrogen and finely ground with an electric grinder to form the seed flour. The experimental design used was completely randomized, in a 2 × 5 factorial scheme (vigor levels × stress times), with four replications. All biochemical analyses were conducted in triplicate. Analysis of variance (F Test) was performed, and the means of the seed lots were compared using the Tukey's test ($p < 0.05$) and Sisvar statistic software. Regression analysis was performed to characterize the behavior of variables according to the periods of stress.

α-amylase activity

The α-amylase activity was measured based on the 3,5-dinitrosalicylic acid (DNS) method described by Miller (1959). To obtain the enzyme extract, 250 mg of seed flour was added to 5 mL of sodium acetate (pH 5.5 to 100 $mmol \cdot L^{-1}$) + 10 $mmol \cdot L^{-1}$ $CaCl_2$. After that, the samples were subjected to shaking in an ice bath for 1 hour. The extracts were centrifuged for 5 minutes. Aliquots of 2 mL of the enzyme extract were placed in a water bath for 15 minutes at 70ºC to inactivate other enzymes. Incubation was performed with 250 µL of enzyme extract, 250 µL of sodium acetate buffer solution (100 $mmol \cdot L^{-1}$) containing 10 $mmol \cdot L^{-1}$ calcium chloride (pH 5) and 2% starch. The samples were incubated in a water bath for 20 minutes at 38ºC. The reaction was stopped with the addition of 500 µL of DNS solution, and the samples were subsequently kept in a water bath for 6 minutes at 95°C. At the end of this process, 4 mL of distilled water was added. The reading was carried out in a spectrophotometer with an absorbance of 540 nm, and the results were expressed in units of enzyme per milligram of protein ($U \cdot mg^{-1}$ of soluble protein). A standard curve with known concentrations of maltose was used to quantify the activity.

Soluble protein

Using Bradford's (1976) methodology, the soluble protein was measured with the enzyme extract used for α-amylase activity. Twenty µL of diluted sample (1:5 in distilled water), 780 µL of distilled water and 200 µL of Bradford reagent were used for quantification. The absorbance evaluation was carried out in a spectrophotometer at 535 nm. The standard curve was performed with known concentrations of bovine serum albumin (BSA).

Total soluble sugars

For total soluble sugars (TSS), the methodology by Clegg (1956) was used, with some modifications. The seed flour was dried in an oven with air circulation at 50°C for 36 hours. After this process, 100 mg of dry sample were added to 3 mL of 80% ethanol and stirred in a Vortex. After shaking, the samples were incubated in a water bath at 65°C for 20 minutes. After incubation, the materials were centrifuged for 5 minutes at 10,000 rpm. The supernatant was stored, and the extraction process was carried out two more times. The supernatants were mixed, and 50 µL of the aliquot was mixed with 950 µL of distilled water and 3 mL of anthrone reagent, after vortexing for 5 seconds. The samples were placed in a water bath for 7.5 minutes at the temperature of 95°C, and after this period the reaction was stopped using an ice bath. The absorbance was read using a spectrophotometer at 630 nm. For quantification, a curve was carried out with five known doses of glucose.

Soluble sugars from the leachate

The solution of leachates from the electrical conductivity analysis was used, which after 24 hours of analysis was collected and stored. Quantification was carried out using a methodology like that carried out for seeds, but without the extraction process.

Proline

Proline was performed using the method of Bates et al. (1973), i.e., 250 mg of seed flour was macerated with 5 mL of 3% sulfosalicylic acid. After maceration, the extracts were centrifuged for 15 minutes, and the supernatant was collected. For quantification, 1 mL of the extract, 1 mL of acid ninhydrin, and 1 mL of glacial acetic acid were used, which were incubated at 95°C for 60 minutes. After incubation, the samples were cooled, and 2 mL of toluene was added. The analytes were then vortexed for 10 seconds and allowed to rest for 10 minutes. After this period, the supernatant produced in the reaction was aspirated and analyzed using a spectrophotometer at 520 nm in glass cuvettes. Data were quantified from a curve with known proline concentrations.

Hydrogen peroxide

Using the methodology based on that described by Velikova et al. (2000), 500 mg of seed flour was added to 5 mL of 0.1% TCA. The extract was macerated and then centrifuged for 10 minutes. For quantification, 0.5 mL of sample, 0.5 mL of phosphate buffer (50 mM, pH 7.0) and 1 mL of 1M potassium iodide were used. The analyte was kept in the dark for 30 minutes before readings. The hydrogen peroxide content was determined from a standard curve of H_2O_2, and the spectrophotometer reading was performed at a wavelength of 390 nm.

Catalase analysis

For catalase analysis, Aebi's (1984) methodology was used, i.e., 250 mg of previously ground seeds were used, with 2.5 mL of potassium phosphate buffer to form the enzyme extract. The extraction was carried out while stirring in an ice bath. After extraction, the extract was centrifuged for 10 minutes. The reaction was prepared directly in a quartz cuvette, using 2,100 µL of phosphate buffer, 800 µL of a 75 mM H_20_2 solution and 100 µL of sample, in total 3 mL, and the reading was taken from 0 to 120 seconds after pipetting at 240 nm. Quantification was based on the H2O2 extinction coefficient, and the results were expressed in µmol $min^{-1} \cdot mg^{-1}$ of protein.

Lipid peroxidation

Lipid peroxidation was assessed based on the quantification of malondialdehyde (Hodges 1999). Fifty mg of seed flour was used, and extraction with 1 mL of 80% ethanol, followed by the addition of 4 mL of water and centrifugation for 5 minutes. For quantification, 0.7 mL of sample, 0.7 mL of TCA + TBA were used. The analytes passed through a water bath at 95°C for 25 minutes. After incubation, centrifugation and reading at 532 and 600 nm on a spectrophotometer in a glass cuvette took place.

Carotenoid

Carotenoid was carried out using the methodology developed by Wellburn et al. (1994). Three hundred mg of seeds were added to 3 mL of methanol. The extraction was carried out under shaking for 1 hour, and then the extracts were placed in a freezer for 16 hours. After this period, the samples were centrifuged for 10 minutes. The reading was taken at 470 nm in a spectrophotometer in glass cuvettes.

RESULTS AND DISCUSSION

The artificial reduction of vigor was effective since there was reduction in the percentage of germination and vigor by accelerated aging and vigor index tests (Table 1). For the high-vigor lot, the percentage of normal seedlings in the first count reached values very close to the final count, as the seed lot presents high speed and uniformity of germination. Differences were observed between lots for all variables analyzed, both germination and vigor. However, the difference between the percentage of normal seedlings obtained in the germination test was significantly smaller compared to that obtained in the accelerated aging test. These results also indicate that differences in seed vigor don't depend exclusively on different genotypes; they also depend on the deterioration state of the seed.

Table 1. Germination and vigor of high- and low-vigor lots based on the parameters of germination percentage, first germination count, accelerated seed lots, and vigor index*.

Seed lots	Germination (%)	First germination count (%)	Accelerated aging (%)	Vigor index
High vigor	99 a	97 a	85 a	843 a
Low vigor	92 b	88 b	60 b	723 b
CV (%)	3.3	3.4	6.3	6.6

*Means followed by the same letter do not differ from each other by the Tukey test ($p < 0.05$); CV: coefficient of variation.

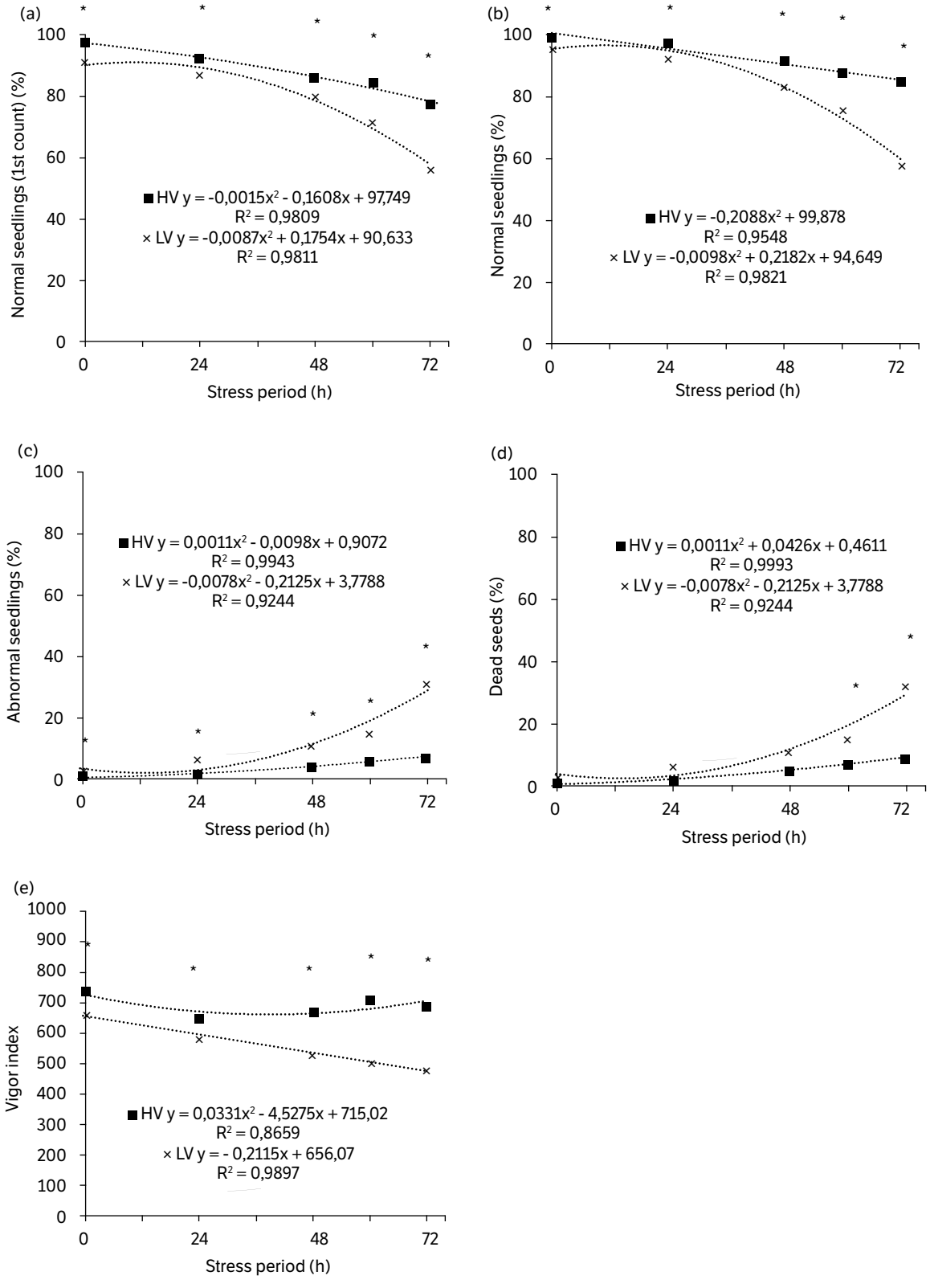
When comparing the seed lots during accelerated aging, reduction was observed in the percentage of normal seedlings in both counts, both in high- (by 14% on the second count) and low-vigor seeds (by 38% on the second count) (Figs. 2a and 2b). Furthermore, higher levels of abnormal seedlings were observed for low-vigor seeds for all periods of stress (Fig. 2b), with increasing levels as stress increased for both lots. Differences were observed between lots with respect to dead seeds percentage only for 60 and 72 hours of stress. Regarding the vigor index, seeds with high vigor obtained higher values in all periods of stress (Fig. 2e). The behavior of the vigor index for low-vigor seeds showed a decreasing trend, while that of high-vigor seeds was relatively stable.

In general, reduction in physiological performance due to stress caused by high temperature and humidity occurred by accelerating seed deterioration (Navarro et al. 2015). Xu et al. (2023) also obtained reduction in the physiological performance in two cultivars of maize seeds when they were submitted to accelerated aging. Thus, the initial state of seed deterioration, before exposure to stress, interferes with the seed's response to this process. Therefore, it was shown in this study that vigor is an important attribute in overcoming stressful conditions before and during emergence.

For electrical conductivity, no statistical differences were observed among lots or periods of stress (Fig. 3a). Due to the conditions of 45°C and saturated humidity, solute leaching may have already occurred during the stress treatment, because they already started imbibition and reorganization of the membranes (Marcos-Filho 2015). Therefore, membrane damage couldn't be evaluated in these conditions. The electrical conductivity is a test that is not fully established for evaluating seed vigor, as it presents conflicting results depending on the initial conditions of the seeds, such as seed moisture and storage temperature (Panobianco and Vieira 2007, Marcos-Filho 2015).

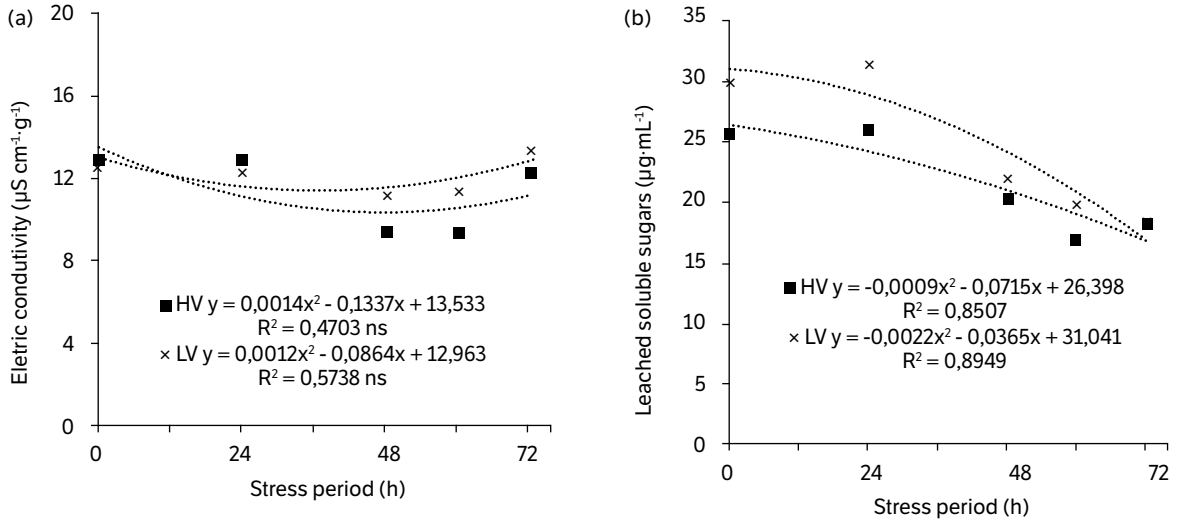
As for the leached soluble sugars, both seed lots showed reduced leakage as periods of stress progressed (Fig. 3b). The conditions prior to carrying out the stress test indicate that the seeds that have gone through longer periods of stress have already started the germination process due to the high humidity condition, having gone through phase I of germination, in which seed imbibition and reorganization occur. This causes sugar leaching to decline as the stress period increases. Furthermore, during periods of stress, due to increases in respiratory activity, the seeds consume sugars, leaving less of them free to be leached (Marcos-Filho 2015).

Alpha-amylase activity showed similar behavior between seed lots during periods of 24, 48 and 60 hours of stress, with differences observed only under no stress condition and in the longer period of stress (72 hours). Under no stress conditions, seeds with low vigor showed greater enzyme activity than high-vigor seeds, likely due to the process of artificial reduction of vigor. For seeds that underwent 72 hours of stress, high-vigor seeds showed higher alpha-amylase activity (Fig. 4a).



*Significant difference between vigor lots by the Tukey's test ($p < 0.05$).

Figure 2. Physiological performance of seedlings from high- (HV) and low-vigor (LV) seed lots subjected to different periods of stress due to accelerated aging.



*Significant difference between seed lots by the Tukey's test ($p < 0.05$).

Figure 3. Electrical conductivity and leached soluble sugars from high- (HV) and low-vigor (LV) seed lots subjected to different periods of stress due to accelerated aging.

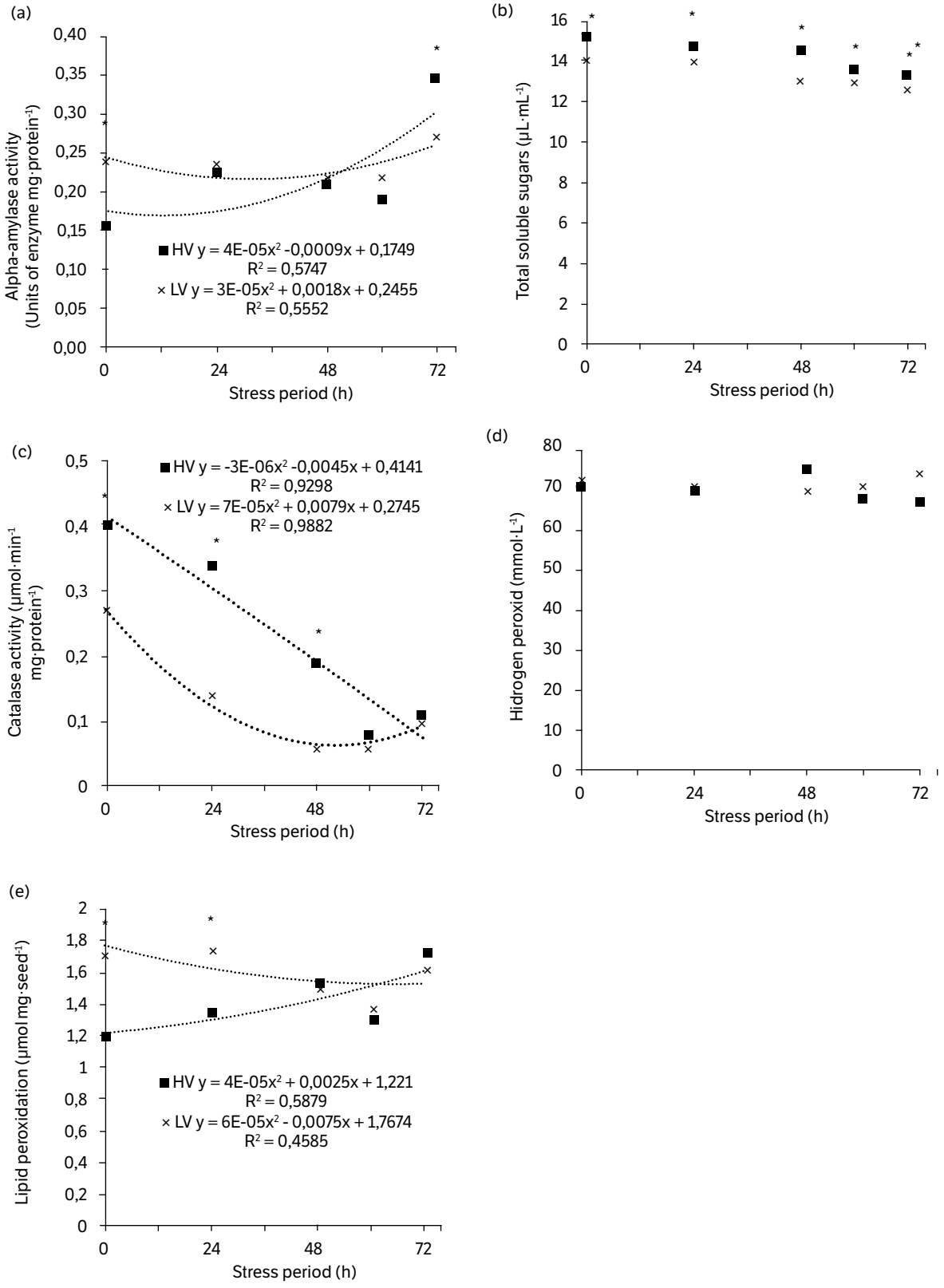
Several studies confirm the correlation between seed vigor and alpha-amylase activity (Heberle et al. 2019, Nerling et al. 2022, Padilha et al. 2022). The greater alpha-amylase levels in high-vigor seeds can be explained by two issues. The first is that the proportion of dead seeds in the low-vigor seeds under these conditions is significantly higher than in the low-vigor seeds, causing an activity dilution effect (Fig. 2d). Furthermore, high-vigor seeds showed greater alpha-amylase activity to likely hydrolyze and mobilize soluble sugars to repair the damage caused by stress (Nerling et al. 2018, Padilha et al. 2022).

Regarding the total soluble sugar content, there were no differences between the stress periods (Fig. 4b). However, for this variable, a trend of higher values was observed for the high-vigor seed lot. High-vigor seeds have higher levels of soluble sugars in general (Nerling et al. 2018, Andrade et al. 2020). This factor may partly explain why, regardless of stress conditions, these seeds present better physiological performance. Thus, it can be inferred that the availability of soluble sugars, despite being highly dependent on the seed genotype, is highly influenced by the reduction of vigor.

Catalase activity was higher for high-vigor seeds for the control and for the 24 and 48 hours of stress (Fig. 2c), showing a decreasing trend for both lots. Catalase is an enzyme that has high sensitivity to temperature (Eyster 1950). In this respect, the reduction in its activity was likely due to the exposure to stress by high temperature. Other studies have also observed reduction in catalase activity with the progression of deterioration in corn seeds (Timóteo and Marcos-Filho 2013, Heberle et al. 2019, Xu et al. 2023). Thus, it is observed that high-vigor seeds likely obtained greater protection against damage caused by free radicals at milder levels of stress, but that at more extreme stress periods catalase did not maintain its greatest activity. This indicates that there is little contribution of catalase activity to protect seeds from deterioration during periods of high temperature and humidity stress.

For lipid peroxidation, the behavior differed between lots (Fig. 4d). A significant difference was observed only for the control and for 24 hours of stress, with lower peroxidation for high-vigor seeds, while in the other periods lipid peroxidation was similar between seed lots. In other studies, differential behaviors of lipid peroxidation were found according to stress, whether declining or increasing (Azooz 2009, Xu et al. 2023). Therefore, lipid peroxidation cannot be indicated as a process that explains the better performance of seeds with greater vigor subjected to stress.

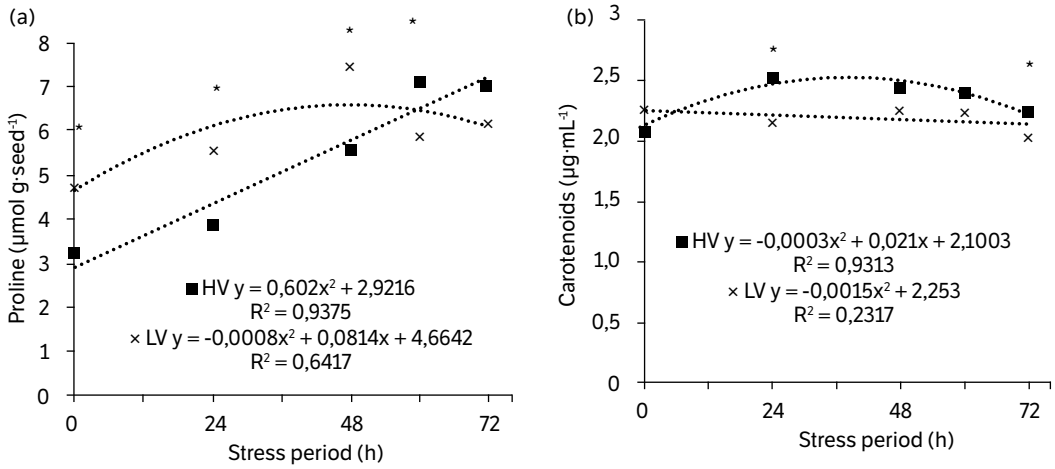
No differences were observed between lots or between stress levels with respect to hydrogen peroxide quantifications (Fig. 4e). Some other studies have found an increase in the amounts of reactive oxygen species when seeds were subjected to accelerated aging stress in corn (Xu et al. 2023) and rice (Zheng et al. 2024). However, as the seed presents other forms or reactive oxygen species, it cannot be inferred from our results that there was no greater oxidative damage during periods of stress.



*Significant difference between seed lots by the Tukey's test ($p < 0.05$).

Figure 4. Alpha-amylase activity, total soluble seed sugars, catalase activity, hydrogen peroxide, and lipid peroxidation of high- (HV) and low-vigor (LV) seed lots subjected to different periods of stress due to accelerated aging.

In the comparison between the treatment lots, a superior proline production was observed on the low-vigor seeds for the control, 24 and 48 hours of stress. From this point onwards an inversion was observed: high-vigor seeds started to produce more proline in comparison (Fig. 5a) to low-vigor seeds. However, at the longest period of stress (72 hours), no significant difference was observed between lots.



*Significant difference between seed lots by the Tukey's test ($p < 0.05$).

Figure 5. Quantification of proline and carotenoids in seedlings from high- (HV) and low-vigor (LV) seed lots subjected to different periods of stress due to accelerated aging.

Low-vigor seeds initially had a greater amount of proline as they are more susceptible to stress, but this production did not allow reducing the effect of stress, especially at the more extreme levels. High-vigor seeds accumulated more proline during most extreme periods of stress. Thus, proline cannot be directly related to stress tolerance in high-vigor seeds because no significant difference was observed between seed lots at the longest stress period. Padilha et al. (2022) couldn't find association of proline levels and seed vigor or tolerance to stressful conditions either.

The behavior of the carotenoid content in high-vigor seeds throughout the stress periods was similar to that observed for low-vigor seeds (Fig. 5b), with differences only observed during 24 and 48 hours of stress, and in these cases the seeds of high vigor showed superiority.

Carotenoids have a reportedly antioxidant effect on seeds by preventing the production of reactive oxygen species (Taiz et al. 2017). For the differences observed in the current experiment, this component cannot be directly related to the greater tolerance of high-vigor seeds to stress, as no reduction in hydrogen peroxide or lipid peroxidation was observed during the periods in which there was a higher carotenoid content.

High-vigor seeds showed better performance in all physiological variables and at all stress levels compared to low-vigor seeds, demonstrating their greater tolerance in responding to stress conditions. An analysis of the components of antioxidant metabolism did not present sufficient evidence that they represent a strategy for high-vigor seeds in this greater tolerance. However, a high-amylase activity and total soluble sugars during stress indicate that better starch reduction and sugar availability are strategies for the improved stress tolerance observed on high-vigor seeds. From this perspective, the availability of soluble sugars in seeds may be the differential aspect of high-vigor seeds to tolerate stress, and future studies can reveal which sugars are more influent in this process.

CONCLUSION

High-vigor maize seeds better tolerate stress conditions caused by high temperature and humidity.

The higher content of total soluble sugars and alpha-amylase activity may explain the better performance of high-vigor seeds.

CONFLICT OF INTEREST

Nothing to declare.

AUTHORS' CONTRIBUTION

Conceptualization: Silva, M. B. P. and Coelho, C. M. M. **Formal analysis:** Silva, M. B. P., Coelho, C. M. M. and Siega, Y. P. **Investigation:** Silva, M. B. P. and Siega, Y. P. **Methodology:** Silva, M. B. P., Coelho, C. M. M. and Siega, Y. P. **Writing – original article**: Silva, M. B. P. **Writing – review & editing:** Silva, M. B. P., Coelho, C. M. M. and Siega, Y. P.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

FUNDING

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
Finance Code 001

Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina
Grant No: 2023TR332

Conselho Nacional de Desenvolvimento Científico e Tecnológico
Grant No: PQ1C

ACKNOWLEDGMENTS

To Universidade do Estado de Santa Catarina for support during the research.

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