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Impact of GA_3 on Sugar and Lipid Degradation during *Annona x atemoya* Mabb. Seed Germination

Carolina Ovile Mimi [1], Marília Caixeta Sousa [1], Patrícia Luciana Carriel Corrêa [1], Ivan De-la-Cruz-Chacón [2], Carmen Sílvia Fernandes Boaro [1] and Gisela Ferreira [1,*]

[1] Department of Biodiversity and Biostatistics, Institute of Biosciences, São Paulo State University (Unesp), Prof. Dr. Antônio Celso Wagner Zanin Street, 250, Botucatu 18618-689, SP, Brazil
[2] Laboratorio de Fisiología y Química Vegetal, Instituto de Ciencias Biológicas Universidad de Ciencias y Artes de Chiapas Libramiento Norte-Poniente 1150, Tuxtla Gutiérrez 29039, CHIS, Mexico
* Correspondence: gisela.ferreira@unesp.br; Tel.: +55-(014)-38800114

Abstract: Gibberellins act to overcome dormancy and increase the germination rate of seeds of several species, including the genus *Annona*. Considering that *Annona* seeds have a high lipid content and have few sugars, the degradation of such reserves from the application of gibberellins has not been described so far. This study aimed to evaluate how the application of different gibberellic acid (GA_3) concentrations acts on the sugar and lipid degradation pattern during the germination of atemoya seeds (*Annona x atemoya* Mabb.). Therefore, two experiments were carried out, one to evaluate the effect of GA_3 on the germination process and another to evaluate the degradation of the reserves. To study the effect of GA_3 on germinability, four treatments with GA_3 concentrations of 0, 250, 500, and 1000 mg L^{-1} were used. To study the degradation of reserves, the four GA_3 concentrations and five collection times were used (dry seed; seed with 1 day, 5 days, and 10 days of water acquisition; and seeds with primary root emission). Atemoya seeds showed an increase in germinability and changes in the sugar and lipid degradation pattern during the germination process in response to the treatments with GA_3. Lipid and sugar degradation was observed from 24 h after seed immersion in GA_3. The highest GA_3 concentrations (500 and 1000 mg L^{-1}) led to increases of 25% and 20%, respectively, in the germination rate, intensification of lipid degradation in seeds with primary root emission, and a decrease in sugar concentration until the 5th day.

Keywords: *Annona*; germination; reserve mobilization; lipids; sugars; gibberellins

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1. Introduction

The *Annona* genera, with approximately 166 species (79 found in Brazil) [1,2], is relevant in the Annonaceae family due to the high commercial value of species with fruits such as *Annona muricata* (soursop), *Annona x atemoya* Mabb. (atemoya), *Annona squamosa* (custard apple), and *Annona cherimola* (cherimoya) [3–5], as well as being an important source of bioactive molecules for the agrochemical and the pharmaceutical industries [6–9].

Annona seeds generally have a low and uneven germination, in addition to numerous reports of dormancy, related to morphological and/or physiological causes [10–13]. From the physiological point of view, the hormonal balance between germination inhibitors such as abscisic acid (ABA) and germination promoters such as gibberellin (GA) regulate the germination process, either by maintaining dormancy or promoting germination [14,15]. More specifically, it is observed that gibberellins promote the production and/or reactivation of hydrolytic enzymes such as α-amylase, hydrolases, and proteases involved in the solubilization of endosperm reserves in order to release energy for germination to occur with resumption of the embryo development [16–18].

Thus, plant regulators can act to overcome dormancy, accelerating the emergence speed and help to express the germination potential of seeds of various species [15,19].

In this context, several studies have been developed with gibberellins to overcome the dormancy of *Annona* seeds, such as *Annona macroprophyllata*, *Annona purpurea* [12], *Annona squamosa* L. [20,21], and *Annona x atemoya* Mabb. [22].

The treatments with plant regulators are carried out during the imbibition of seeds, a period in which there is an increase in metabolism, which results in the supply of the energy and nutrients necessary for resuming the growth of the embryo axis [23]. In *Annona* seeds, imbibition varies from 5 to 70 h [24,25]. After imbibition, there is a period of stability in water acquisition when substances such as sugars and lipids [26] are transported from the reserve tissue to the meristematic tissue. These are later reorganized into complex substances that form the protoplasm and cell walls, promoting the growth of the embryo axis with the emission of the primary root, and leading to the end of germination and the beginning of the seedling development [27]. The emission of the primary root in *Annona* occurs approximately 234 h (9 days) after the beginning of imbibition [25].

The literature clearly presents the effect of gibberellin in overcoming dormancy and in the degradation of starch reserves [23,28]; however, there are few reports of the action of gibberellin applied exogenously in the metabolism of seeds with a high percentage of lipid reserve [19]. In this context, the purpose of this work was to understand how gibberellin, which is known to overcome the dormancy and increase the germination process of *Annona* seeds [12,13,29–32], acts in the degradation and mobilization of the lipid reserve, since seeds of this genus present abundance of this type of reserve, ranging from 20 to 48% of the dry seed weight [33–35], and about 3.5% of sugars [13]. Therefore, this study will describe how the degradation and mobilization of lipids and sugars occur during the germination process from an exogenous GA_3 supply, which has not yet been described for the *Annona* genera.

The present study was carried out with atemoya seeds (*Annona x atemoya* Mabb.), one of the main commercial *Annona* from the Annonaceae family, which has been gaining ground in the fruit-growing activity of Brazil, Chile, Mexico, Venezuela, and Australia [4], with seeds being used to produce rootstock in order to ensure compatibility between scion and rootstock in seedling production [36]. Atemoya seeds have an abundant, ruminate, hard, oily endosperm and a small straight embryo [37]. In addition, atemoya seeds have a low-permeability tegument and physiological dormancy, which lead to a slow and uneven germination that can be overcome with plant growth regulator treatments such as gibberellin [31,36]. Therefore, we hypothesize that the application of an exogenous proportion of gibberellin should modulate the degradation of the lipid and sugar reserves that help the gemination of atemoya seeds.

2. Materials and Methods

To obtain seeds, ripe fruits of 'Thompson' atemoya (*Annona x atemoya* Mabb.) were collected, with an average weight of 281.141 g, height of 84.84 mm, and diameter of 75.68 mm, in a commercial orchard located in the municipality of Pardinho—São Paulo, Brazil, (coordinates: Latitude −23.104611, Longitude −48.377639 23°06′16.6″ S 48°22′39.5″ W and climate classification: Cwb). After extraction, a sample of the seed lot was used to determine the initial moisture content of the seeds by the oven method, 105 ± 3 °C for 24 h, adopting four 4 replicates of 25 seeds [38], and the values obtained were, on average, 27.99% water. The group of seeds used for the treatments were disinfected with a 1% sodium hypochlorite solution and a 4% Orthocide fungicide and remained for seven days on a bench for drying. After this period, the moisture content (8.65%) was determined by the oven method, 105 ± 3 °C for 24 h, adopting 4 replicates of 25 seeds [38].

2.1. Germination Test

The experiment was carried out in a completely randomized design, with 4 treatments and 4 replicates of 25 seeds [32]. Treatments consisted of immersion of seeds for 36 h [31] in gibberellic acid (GA_3) solutions at concentrations of 0, 250, 500, and 1000 mg L^{-1}, i.a. During the imbibition period, the solutions with the seeds received constant aeration using aquarium pumps and were kept in a laboratory at a temperature of 25 °C (±2 °C). As a

source of gibberellin, the commercial product Pro-Gibb® 400 was used, which is composed of 40% GA_3 in the form of a soluble powder. Subsequently, seeds were sown on a roll of germination paper moistened with 2.5 times its weight in distilled water and kept in a germinator with alternating temperature and photoperiod (20 °C for 8 h of dark, 30 °C for 16 h of light).

Every 2 days, from the beginning of the experiment implementation until the ending at 35 days (constant germination), evaluations were carried out on germinated seeds that emitted at least 2 mm of primary root [32,39]. The characteristics evaluated were: germination rate (%G), germination speed index (GSI) [13,40], mean germination time (MGT) [41], and germination frequency and synchronicity (U) to evaluate how dispersed germination is over time, demonstrating whether germination is homogeneous or heterogeneous in relation to each treatment [30,42].

2.2. Reserve Degradation

To study reserve degradation, a completely randomized design was used with 4 replicates per plot in a 4 × 5 factorial scheme, with four GA_3 concentrations (0, 250, 500, and 1000 mg L^{-1}) and five collection times (T) [T1—dry seeds (before the beginning of imbibition); T2—seeds with 1 day (24 h) of water acquisition (imbibition); T3—seeds with 5 days (120 h) of water acquisition; T4—seeds with 10 days (240 h) of water acquisition; T5—seeds with primary root emission (15 days—360 h, end of germination)].

Collection times were determined according to phases established in the water acquisition curve proposed in the study by Ferreira et al. [25]. After treatments, seeds were kept in a germination roll under the same temperature and photoperiod conditions as in the germination test. At each time point, seeds were collected, and the endosperms were removed, frozen, and macerated with the aid of liquid nitrogen for the determination of lipids and sugars.

2.3. Extraction and Quantification of Total Lipids

Total lipids were extracted according to Manirakiza et al. [43] and Ambalkar et al. [44]. Endosperm samples (approximately 2 g per replicate) were placed with 100 mL of hexane in a Soxhlet flask for extraction for three eight-hour periods. At each extraction period, the supernatant was filtered and taken to be concentrated and stored in properly labeled and weighed flasks. Quantification was obtained by the weight difference between the lipid extract and the dry mass (DM) of the endosperm (g of lipid/g of DM).

2.4. Extraction and Quantification of Total Soluble Sugars and Sugar Profile

The extraction of total soluble sugars was performed according to Garcia et al. [45]. Endosperms were macerated in liquid nitrogen and stored in an ultra-freezer until analyses were performed. For extraction, samples were weighed and 100 mg of endosperm were used per replicate in 2 mL eppendorf, 1 mL of 80% ethanol was added, and samples were vortexed. Subsequently, extraction was carried out by boiling in a water bath at 80 °C for fifteen minutes to inactivate enzymes. Then, samples were centrifuged at 12,000 rpm and 25 °C for fifteen minutes and the residue was extracted twice more with 80% ethanol for fifteen minutes at 80 °C. The combination of extracts will result in the total sugar fraction. Extracts were kept in refrigerator (4 °C) until quantification, where colorimetric analysis was performed using the phenol-sulfuric method, with triplicates of each replicate [46].

One ml of sample was separated for purification in columns containing Dowex cation and anion exchange resins, eluted with 10 volumes of deionized water. The purified material had its pH neutralized with ammonium hydroxide and concentrated until complete drying in a freeze drier. Samples were then resuspended in 5 mL of deionized water and analyzed in anion-exchange liquid chromatography with pulsed amperometric detection (HPAEPAD) (Dionex CarboPacTM PA−100 Column, 4 × 250 mm) with an elution gradient of Sodium Hydroxide (625 mM), Ultrapure water (Milli Q), and Sodium Acetate (0.5 M). Eight sugars (arabinose, fructose, glucose, mannose, raffinose, sucrose, stachyose, and

trehalose) were analyzed, and the results were expressed in micrograms per gram of dry mass (μg g^{-1} DM).

2.5. Statistical Analysis

Data were submitted to the normality test and homogeneity of variance. After which, the germinability data were analyzed using a one-way ANOVA analysis of variance and the reserve degradation data were analyzed using a two-way ANOVA analysis of variance. Means were compared using the Tukey test ($p \leq 0.05$).

3. Results

3.1. Germinability

Atemoya seeds showed increased germinability and changes in the pattern of sugar and lipid degradation from the beginning of imbibition in response to GA_3 treatments.

The highest GA_3 concentrations (500 and 1000 mg L^{-1}) led to increases of 25% and 20%, respectively, in the germination rate compared to the control treatment (0 mg L^{-1}) (Table 1). No treatment changed the average germination time; however, the concentration of 500 mg L^{-1} provided a higher germination speed index (2.75) when compared to the control and GA_3 concentration of 250 mg L^{-1} (1.74 and 1.75, respectively).

Table 1. Germination rate (%), mean germination time (MGT), germination speed index (GSI), and germination synchronization (U) of atemoya seeds (*Annona x atemoya* Mabb.) submitted to treatments with different GA_3 concentrations.

GA_3 [mg L^{-1}]	G (%)	MGT (Days)	GSI	U
[0]	51.00 ± 6.83 b	8.39 ± 0.92 a	1.74 ± 0.30 b	0.14 ± 0.01 a
[250]	59.00 ± 8.87 ab	9.55 ± 0.50 a	1.75 ± 0.38 b	0.13 ± 0.02 a
[500]	75.75 ± 5.91 a	8.57 ± 0.83 a	2.75 ± 0.45 a	0.15 ± 0.01 a
[1000]	71.00 ± 12.38 a	9.06 ± 0.63 a	2.15 ± 0.40 ab	0.13 ± 0.02 a
p	0.007 **	0.169 $^{n.s}$	0.010 **	0.275 $^{n.s.}$
F	6.48	1.99	6.03	1.46
C.V. (%)	13.79	8.30	18.38	13.94

Results are presented as the mean value ± the standard deviation. The values were statistically tested using a one-way ANOVA. Means followed by the same letters do not differ by the Tukey test at 5% probability and compare concentrations. *p* and F values (ANOVA) are indicated. Analyzed the effect of concentrations of GA_3 on germination rate (%), mean germination time (MGT), germination speed index (GSI), and germination synchronization (U). $^{n.s.}$: not significant (*p*-value > 0.05); ** 1% significance (*p*-value ≤ 0.01).

Synchronization values (U), which indicate how concentrated germination is over time [42], were not altered by treatments with different concentrations of GA_3, but the values were near zero, demonstrating that seed germination was concentrated at some point during the evaluation time (Table 1). The relative frequency of germination demonstrates the homogeneity or heterogeneity of germination, where the peak represents the moment with the highest number of germinated seeds and may be unimodal (one germination peak) or polymodal (two or more germination peaks) [42]. The results demonstrate that with the use of the lowest concentration of GA_3 (250 mg L^{-1}) the frequency of germination occurred more spaced over time, with the presence of more germination peaks (polymodal) when compared to the other concentrations, thus demonstrating the heterogeneity of germination with this treatment. On the other hand, the use of the highest concentration of GA_3 (1000 mg L^{-1}) shows the peak of germination more evident at the beginning of the germination process, where a greater number of seeds germinated in the same period, demonstrating more homogeneous germination (Figure 1).

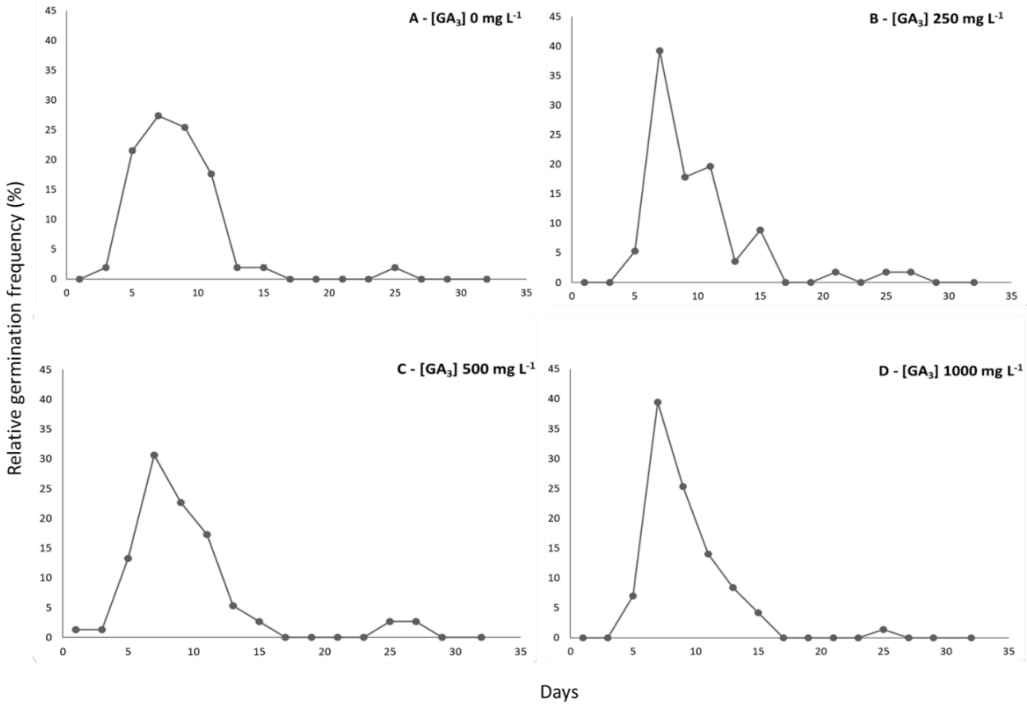

Figure 1. Relative germination frequency of atemoya seeds (*Annona x atemoya* Mabb.) submitted to treatment with different GA_3 concentrations ((**A**)—0 mg L^{-1}; (**B**)—250 mg L^{-1}; (**C**)—500 mg L^{-1}; and (**D**)—1000 mg L^{-1}).

3.2. Lipids

In atemoya seeds, continuous lipid degradation was observed from 24 h after the immersion of seeds in treatments. At 15 days after the beginning of treatments, the application of the highest GA_3 concentrations (500 and 1000 mg L^{-1}) intensified lipid degradation (35–38% of initial content) (Table 2).

Table 2. Total lipid concentration (mg g^{-1} DM) in atemoya seeds submitted to 0, 250, 500, and 1000 mg L^{-1}, i.a., of GA_3 over five collection times.

GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 Day	T3—5 Days	T4—10 Days	T5—15 Days
[0]	274.68 ± 7.17 a A	210.65 ± 16.14 a BC	211.03 ± 5.45 a BC	187.73 ± 18.72 a C	219.25 ± 6.08 a B
[250]	274.68 ± 7.17 a A	192.00 ± 15.58 a BC	209.25 ± 13.48 ab B	167.03 ± 13.31 ab C	218.13 ± 25.06 a B
[500]	274.68 ± 7.17 a A	216.95 ± 7.21 a B	221.73 ± 10.44 a B	186.23 ± 3.56 a C	179.53 ± 15.51 b C
[1000]	274.68 ± 7.17 a A	204.23 ± 25.08 a B	185.10 ± 14.41 b BC	160.70 ±11.34 b C	170.13 ± 12.22 b C
GA_3 *p*: 0.0001 **; F: 8.236		Days *p* < 0.001 **; F: 109.095		GA_3 × Days *p*: 0.0003 **; F: 3.729	

Results are presented as the mean value ± the standard deviation. The values were statistically tested using a two-way ANOVA. Means followed by the same letters, lowercase (to compare GA_3 concentrations within each collection time) and uppercase (to compare the different collection times at each GA_3 concentration) do not differ from each other by the Tukey test at 5% probability. *p* and F values (ANOVA) are indicated. Analyzed the interaction between GA_3 (GA_3 concentrations) × Days (collection times) on the concentration of total lipid. ** 1% significance (*p*-value ≤ 0.01).

3.3. Sugars

It was verified that total soluble sugars (Table 3) are present at higher concentration in dry seeds (Time 1) and their degradation was observed from 24 h after the beginning of treatments.

Table 3. Total soluble sugars (mg g^{-1} DM) in atemoya seeds at 0, 250, 500, and 1000 mg L^{-1}, i.a., of GA_3 over five collection times.

GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 Day	T3—5 Days	T4—10 Days	T5—15 Days
[0]	19.90 ± 0.82 a A	13.90 ± 1.41 b B	9.52± 0.13 a C	12.07 ± 1.42 bc BC	11.07 ± 2.23 c BC
[250]	19.90 ± 0.82 a A	17.50 ± 0.53 a B	8.88± 1.18 a C	11.09 ± 1.20 c BC	14.02 ± 1.94 b C
[500]	19.90 ± 0.82 a A	16.41± 1.43 ab B	9.30± 1.94 a D	14.81 ± 2.22 b BC	13.11 ± 2.90 bc C
[1000]	19.90 ± 0.82 a A	16.33± 1.75 ab B	9.22± 0.59 a C	18.12 ± 2.47 a AB	17.20 ± 1.62 a AB
GA_3 $p < 0.001$ **; F: 11.544		Days $p < 0.001$ **; F: 96.985		GA_3 × Days $p < 0.001$ **; F: 4.769	

Results are presented as the mean value ± the standard deviation. The values were statistically tested using a two-way ANOVA. Means followed by the same letters, lowercase (to compare GA_3 concentrations within each collection time) and uppercase (to compare the different collection times at each GA_3 concentration) do not differ from each other by the Tukey test at 5% probability. *p* and F values (ANOVA) are indicated. Analyzed the interaction between GA_3 (GA_3 concentrations) × Days (collection times) on the concentration of total soluble sugars. ** 1% significance (*p*-value ≤ 0.01).

Seeds treated with 250 mg L^{-1} of GA_3 showed a degradation pattern of soluble sugars similar to the control. At GA_3 concentrations of 500 and 1000 mg L^{-1}, it was observed that seeds showed a decrease in the concentration of sugars until the 5th day (~53% of initial content), and from the 10th day onwards, an increase in the concentration of these sugars was observed. It was observed that seeds treated with 1000 mg L^{-1} of GA_3 had the highest concentration of total soluble sugars at 10 and 15 days after the start of the treatments compared to the other GA_3 concentrations.

3.4. Sugar Profile

Of the analyzed sugars, six were detected in the endosperm of atemoya seeds, namely: arabinose, fructose, glucose, mannose, sucrose, and stachyose (Table 4).

The arabinose concentration in atemoya seeds was not influenced by the different gibberellin concentrations, but rather by the collection time, where there was accumulation of this sugar, especially on the 10th and 15th days.

It was observed that the highest GA_3 concentration (1000 mg L^{-1}) caused changes in different sugars when compared to the other treatments. For fructose, there was a decrease of more than 90% in its concentration at the beginning of the imbibition process when compared to baseline, followed by an increase in its concentration on the 5th day when treatment with 1000 mg L^{-1} of GA_3 provided the highest concentration of this monosaccharide. For glucose and mannose, it was observed that in seeds treated with 1000 mg L^{-1} of GA_3, glucose accumulation began on the 1st day of imbibition, with a peak on the 10th day.

Stachyose showed peak concentrations on the 10th and 15th days, and in seeds treated with 1000 mg L^{-1} of GA_3, its lowest concentration was observed, among the other treatments, at the last moment of evaluation. In general, sucrose showed a peak concentration on the 1st day, with a decrease in concentration on the 5th day for the 1000 mg L^{-1} GA_3 treatment.

Table 4. Profile of soluble sugars (μg g^{-1} DM) in atemoya seeds submitted to 0, 250, 500, and 1000 mg L^{-1}, i.a., of GA_3 over five collection times.

Arabinose					
GA_3 [mg L^{-1}]	**T1—Dry Seeds**	**T2—1 Day**	**T3—5 Days**	**T4—10 Days**	**T5—15 Days**
[0]	2.67 ± 0.76 a B	1.33 ± 1.12 a BC	0.76 ± 0.25 a C	1.66 ± 0.89 c BC	7.77 ± 1.49 a A
[250]	2.67 ± 0.76 a C	1.63 ± 0.88 a C	2.26 ± 0.28 a C	7.06 ± 1.11 a A	4.70 ± 1.03 b B
[500]	2.67 ± 0.76 a BC	1.36 ± 0.67 a C	0.98 ± 0.44 a C	3.55 ± 0.30 b B	8.09 ± 1.30 a A
[1000]	2.67 ± 0.76 a AB	1.17 ± 0.67 a B	2.26 ± 0.40 a AB	3.36 ± 1.44 bc A	3.86 ± 1.56 b A
GA_3 *p*: 0.077 **; F: 4.349		Days *p* < 0.001 **; F: 81.009		GA_3 × Days *p* < 0.001 **; F: 13.547	
Fructose					
GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 day	T3—5 days	T4—10 days	T5—15 days
[0]	1.43 ± 0.12 a A	0.08 ± 0.01 a D	0.22 ± 0.08 b CD	0.47 ± 0.03 a B	0.37 ± 0.09 a BC
[250]	1.43 ± 0.12 a A	0.09 ± 0.05 a C	0.31 ± 0.07 b B	0.29 ± 0.06 b B	0.36 ± 0.06 a B
[500]	1.43 ± 0.12 a A	0.08 ± 0.03 a C	0.34 ± 0.08 b B	0.26 ± 0.05 b B	0.26 ± 0.09 a B
[1000]	1.43 ± 0.12 a A	0.08 ± 0.03 a D	0.54 ± 0.11 a B	0.28 ± 0.08 b B	0.38 ± 0.02 a B
GA_3 *p* < 0.001 **; F: 12.273		Days *p* < 0.001 **; F: 1310.822		GA_3 × Days *p* < 0.001 **; F: 10.442	
Glucose					
GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 day	T3—5 days	T4—10 days	T5—15 days
[0]	2.97 ± 1.14 a B	2.25 ± 0.62 b B	4.07 ± 0.42 a B	6.74 ± 1.69 b A	6.29 ± 0.96 a A
[250]	2.97 ± 1.14 a B	2.54 ± 0.89 b B	3.34 ± 0.67 a B	6.72 ± 1.48 b A	7.23 ± 1.82 a A
[500]	2.97 ± 1.14 a B	4.38 ± 1.24 ab AB	4.24 ± 0.53 a AB	5.94 ± 2.21 b A	6.13 ± 0.71 a A
[1000]	2.97 ± 1.14 a C	5.49 ± 1.00 b BC	5.12 ± 1.42 a BC	12.73 ± 3.30 a A	6.49 ± 1.42 a B
GA_3 *p* < 0.001 **; F: 10.972		Days *p* < 0.001 **; F: 42.219		GA_3 × Days *p* < 0.001 **; F: 5.648	
Mannose					
GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 day	T3—5 days	T4—10 days	T5—15 days
[0]	6.90 ± 2.07 a B	11.72 ± 0.52 a B	12.45 ± 0.86 ab B	30.57 ± 1.30 b A	27.51 ± 2.08 a A
[250]	6.90 ± 2.07 a B	9.44 ± 3.30 a B	11.89 ± 2.11 b B	29.28 ± 3.32 b A	32.98 ± 1.75 a A
[500]	6.90 ± 2.07 a C	12.84 ± 1.08 a BC	16.18 ± 1.82 ab B	24.56 ± 9.04 b A	30. 99 ± 4.17 a A
[1000]	6.90 ± 2.07 a D	13.38 ± 1.36 a CD	18.67 ± 2.82 a C	38.01 ± 6.47 a A	29.77 ± 4.38 a B
GA_3 *p*: 0.0149 *; F: 3.781		Days *p* < 0.001 **; F: 181.337		GA_3 × Days *p*: 0.0001 **; F: 4.161	
Sucrose					
GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 day	T3—5 days	T4—10 days	T5—15 days
[0]	153.01 ± 17.42 a AB	142.75 ± 16.37 c AB	196.63 ± 56.74 a A	133.89 ± 14.86 a B	113.23 ± 13.79 a B
[250]	153.01 ± 17.42 a B	153.21 ± 26.32 bc B	216.94 ± 34.25 a A	115.48 ± 29.03 a B	103.09 ± 11.99 a B
[500]	153.01 ± 17.42 a ABC	206.70 ± 62.69 ab A	160.65 ± 46.19 ab AB	103.54 ± 21.94 a BC	97.57 ± 4.37 a C
[1000]	153.01 ± 17.42 a B	256.32 ± 52.21 a A	102.95 ± 9.63 b B	129.22 ± 46.17 a B	138.42 ± 15.72 a B
GA_3 *p*: 0.7590 n.s.; F: 0.392		Days *p* < 0.001 **; F: 18.100		GA_3 × Days *p* < 0.001 **; F: 6.462	
Stachyose					
GA_3 [mg L^{-1}]	T1—Dry Seeds	T2—1 day	T3—5 days	T4—10 days	T5—15 days
[0]	0.33 ± 0.04 a B	0.33 ± 0.09 a B	0.62 ± 0.14 a B	2.38 ± 0.72 ab A	2.76 ± 0.51 a A
[250]	0.33 ± 0.04 a B	0.21 ± 0.02 a B	0.59 ± 0.01 a B	1.81 ± 0.84 ab A	2.73 ± 0.48 a A
[500]	0.33 ± 0.04 a BC	0.19 ± 0.05 a C	0.16 ± 0.04 a C	1.28 ± 0.43 b B	2.64 ± 1.46 a A
[1000]	0.33 ± 0.04 a B	0.28 ± 0.03 a B	1.07 ± 0.69 a AB	2.00 ± 0.47 a A	1.13 ± 0.41 b AB
GA_3 *p*: 0.0698 n.s.; F: 2.478		Days *p* < 0.001 **; F: 58.636		GA_3 × Days *p*: 0.0009 **; F: 3.368	

Results are presented as the mean value ± the standard deviation. The values were statistically tested using a two-way ANOVA. Means followed by the same letters, lowercase (to compare GA_3 concentrations within each collection time) and uppercase (to compare the different collection times at each GA_3 concentration) do not differ from each other by the Tukey test at 5% probability. *p* and F values (ANOVA) are indicated. Analyzed the interaction between GA_3 (GA_3 concentrations) × Days (collection times) on the concentration of profile of soluble sugars. n.s.: not significant (*p*-value > 0.05); * 5% significance (*p*-value ≤ 0.05); ** 1% significance (*p*-value ≤ 0.01).

4. Discussion

The characteristics observed with atemoya seeds such as the high germination and homogeneity are desirable in the context of seedling production in a nursery since they facilitate the management of plant lots and contribute to the quality of the seedlings. The action of gibberellin (GA_3) in increasing the germinability of atemoya seeds is related to the

fact that this regulator stimulates the synthesis of hydrolytic enzymes, such as α-amylase, hydrolases, and proteases, leading to greater degradation of reserves [19], which can be specifically confirmed with the greater degradation of lipids over time when the highest GA_3 concentrations were used (Table 2).

Even without the use of gibberellic acid (GA_3), lipid degradation occurred from imbibition, but with lower intensities and germination rates than with the use of GA_3, where an increase in the degradation of lipid reserves and germination was observed, confirming the greater availability of carbon skeletons that will guarantee small embryo growth (also in another annonaceous).

The present study demonstrated that the degradation of lipids and sugars in atemoya seeds occurred from 24 h after seed immersion in the different treatments. Our results corroborate those found in the study by Ferreira et al. [13] with *A. macroprophyllata* and *A. purpurea* seeds, where the use of the GA_{4+7} + BA regulator caused a reduction in the lipid content at the beginning of imbibition, which continued steadily until the moment of primary root development, presenting the lowest lipid content on the 15th and 10th days, respectively. Seeds from other families such as *Euphorbia heterophylla* L. showed a reduction of about 50% in lipid levels after 2 to 3 days of sowing [47], coinciding with radicle protrusion. In *Caesalpinia peltophoroides* Benth. lipid levels decreased during the first 10 days of sowing, with complete consumption up to the 20th day [48,49].

Annona seeds have a higher concentration of lipids compared to the other reserves [35]. In atemoya seeds, lipids make up a large percentage of the reserve profile, as can be seen in this study, where the initial concentration of lipids (274.68 mg g^{-1} DM) is 13 times greater than the initial concentration of total soluble sugars (19.90 mg g^{-1} DM). Furthermore, this is the first report of the concentrations of lipids and sugars in atemoya seeds (27.46% and 1.99%, respectively). These lipids are an important source of energy for seed germination, since their complete oxidation yields more than twice as much energy as the hydrolysis of proteins or carbohydrates, per mass unit [18].

The high lipid content of *Annona* seeds has been described in different studies, such as the one carried out by Ferreira et al. [13], where a higher concentration of lipids was observed as reserve substances in *A. macroprophyllata* (48%) and *A. purpurea* (45%) seeds. In *Annona coriacea* seeds, a lipid content of 46% of the dry weight was found [33], in *Annona crassiflora*, 35% of lipids [50], and in *Annona salzmannii*, 25.2% of lipids [51].

The use of GA_3, at 1000 mg L^{-1}, in atemoya seeds promoted greater accumulation of total soluble sugars in the periods of 10 and 15 days when compared to the other treatments which have their origin in lipids, since in the same period, treatment provided less lipid content, indicating greater degradation of this reserve. Glucose and sucrose are the products of the process of lipid mobilization and degradation through de novo biosynthesis via the glyoxylate cycle and gluconeogenesis [52–54].

The data from this experiment suggest that the degradation of total soluble sugars in seeds provided energy for the embryo development until the 5th day after the application of treatments. On the 10th day, there is greater energy demand, as it precedes the emission of the primary root, making the synthesis of sugars necessary. This decrease in the content of soluble sugars during the phases of water acquisition is in agreement with the results of studies using species of the Annonaceae family. Ferreira et al. [13] observed that in *A. macroprophyllata* and *A. purpurea*, the use of plant regulators, in addition to overcoming dormancy, also increases the degradation of total soluble sugars from the first 24 h of imbibition to the 15th day of evaluation (primary root protrusion). Gimenez et al. [29] also observed a reduction in sugar levels during the imbibition of *Annona emarginata* from 43 mg g^{-1} DM (4.3%) when seeds had 20% water to 29 mg g^{-1} DM (2.9%) when they reached 35% water content.

When reduction in the level of sugars occurs, there is a signaling for lipase with degradation of lipids, so that more sugars are formed to maintain embryo metabolism and growth [19,52,55]. Borek et al. [52] demonstrated that low sucrose content increases lipase activity. When different organs of *Lupinus luteus* L seeds were added to medium containing

low sucrose, an increase in lipase activity was observed, reaching the highest peak, whereas when seeds were added to medium containing high sucrose, lipases showed low activity. A similar study carried out by Sun et al. [19] also demonstrated the metabolism of sugars and lipids during germination and supports the results found in this work with atemoya seeds.

Thus, the greater reduction in sugars caused by the use of the highest gibberellin concentration (1000 mg L^{-1}) may have been the signal for the increase in lipid degradation. This fact observed in atemoya seeds may justify the delay in the time for seeds to germinate, since energy is not readily available. The high lipid content of seeds results in the slow formation of sugars in a way that sustains development and at the same time its accumulation, as observed with soluble sugars on the 10th and 15th days. Thus, as energy availability occurs slowly, the emission of the primary root (end of the germination process) occurs only around the 15th day.

For atemoya, among the soluble sugars identified in the profile, there is a higher sucrose concentration, which is accumulated during embryo development. Sucrose is considered important for maintaining the osmotic potential of cells thereby favoring the imbibition process [56], it is efficiently metabolized and serves as an energy source for the growth of the embryo axis [57]. The decrease in sucrose content observed on the 5th day for seeds treated with 1000 mgL^{-1} of GA_3 may be associated with its degradation into fructose and glucose, which showed increases in concentration on the 10th and 15th days after imbibition.

The high germination of atemoya seeds with the application of 1000 mg L^{-1} of GA_3 may be related to the increase in the concentration of the monosaccharides glucose, mannose, and stachyose on the 10th day. This may be an indication of metabolic adjustment in the preparatory phase for the emission of the primary root observed on the 15th day after imbibition. These osmolytes cause a reduction in the internal water potential, which leads to a new entry of water into the seeds along with the emission of the root [58].

5. Conclusions

Gibberellic acid that is used to overcome dormancy in lipid seeds, like Annonaceae seeds (*v. gr Annona x atemoya* Mabb.), modulates the lipid and sugar degradation during germination, with a lipid continuous degradation throughout the germination process, and an increase the sugar concentration after an initial degradation. Therefore, we can conclude that the Gibberellic acid applied to *Annona x atemoya* seeds causes lipid and sugar degradation to sustain the initial metabolism during the imbibition process, and after which the lipid is continuously degraded. This leads to an increase in sugar concentration with the objective of ensuring germination, and ends with the protrusion of the primary root. This phenomenon is more evident at high concentrations of the plant regulator, which also allows a higher and more synchronous germination rate.

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