Coordinated physiological reorganization of growth and reproductive modulation in watermelon (*Citrullus) lanatus* L.) induced by exogenous application of auxins under humid tropical conditions

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Abstract
The commercial production of watermelon (*Citrullus lanatus* L.) increasingly demands strategies capable of improving fruit quality while reducing seed content. The present study evaluated the effects of exogenous auxin application on fruit growth, seed development and physiological integration under humid tropical conditions of the Ecuadorian Amazon. A completely randomized design with three treatments and three replications was established, including a control without auxin application and two concentrations of Flower Tie® (1 and 2 cm^3 L^{-1}). Fruit weight, diameter, length and seed number were quantified, and integrated physiological indicators were developed to characterize reproductive efficiency, fruit expansion and overall hormonal response. Auxin application significantly enhanced fruit development and partially reduced seed formation. The highest dose increased fruit weight from 9.88 to 15.32 kg (+55.1%), fruit diameter from 16.58 to 24.63 cm (+48.6%) and fruit length from 36.36 to 41.40 cm (+13.9%), while reducing seed number from 645.7 to 548.1 seeds per fruit, corresponding to a 15.1% reduction relative to the control. Analysis of variance revealed highly significant treatment effects ($p < 0.0001$), with very large effect sizes across morphometric, reproductive and integrated physiological variables ($\eta^2 = 0.7891–0.9817$; $\omega^2 = 0.7674–0.9790$). The Integrated Hormonal Response Index (IHRI) increased from 0.00 in the control treatment to 33.15 in the highest auxin concentration, indicating a coordinated enhancement of fruit growth and reproductive modulation. Dose–response modeling showed strong quadratic relationships ($R^2 = 0.9024–0.9817$), while principal component analysis explained 97.86% of total variability and revealed a clear physiological gradient linking biomass accumulation and fruit expansion with reduced seed development. These findings demonstrate that exogenous auxin application promotes coordinated physiological reorganization of fruit growth and reproductive processes, representing a promising strategy for improving watermelon fruit quality under tropical production systems.

Keywords: Auxins; Citrullus *lanatus* fruit development; Hormonal regulation; Seed reduction.

Introduction

Watermelon (*Citrullus lanatus* L.) is a horticultural crop of great economic and social importance, widely cultivated throughout the world, especially in Latin America. Since its introduction to the Americas by enslaved people in the 19th century, watermelon cultivation and consumption have evolved, becoming one of the most appreciated fruits for its flavor and hydrating properties (Sousa & Raizada, 2020). According to FAOSTAT data, watermelon production in Ecuador reached approximately 77,000 tons in 2020, with a harvested area of around 5,000 hectares, reflecting the economic importance of this crop in the country (Ribeiro et al., 2024). This crop represents a significant source of income for farmers and contributes to the growing demand for fresh fruit in both local and international markets (Del Carmen Armas-Vega et al., 2025).

However, one of the most significant challenges in watermelon production is the presence of unwanted seeds in the fruit, which can affect consumer acceptance and, consequently, the profitability of the crop. One study indicates that, on average, 68% of consumers prefer seedless varieties, motivating the search for alternatives to produce (Dijkxhoorn et al., 2019)parthenocarpic watermelons.

The application of phytohormones, particularly auxins, has emerged as a promising strategy for addressing this problem. Auxins are plant hormones that regulate various physiological processes, such as fruit growth, development, and ripening (Mwelase et al., 2024). In watermelon, auxin application can induce parthenocarpy, a phenomenon that allows fruit development without fertilization, resulting in seedless fruit (Tian et al., 2023). In this regard, the ability of auxins to influence fruit morphology is well-documented, and these hormones have been observed to increase fruit size, thereby improving its commercial appeal.

Previous studies have shown that the use of auxins can significantly reduce the number of seeds in various crops. For example, Sosnowski et al. (2023) reported that the application of indole-3-butyric acid (IBA) to

melons resulted in a 45% decrease in seed number, suggesting that auxins can inhibit seed formation in various fruit species. Similarly, Zhang et al. (2022) reported that auxin treatment in tomatoes not only reduced the number of seeds by 30% but also improved fruit quality, highlighting the potential of these hormones in agricultural production

In Ecuador, most farmers lack the necessary knowledge about the use and application of phytohormones in their crops, which limits their ability to maximize yield and product quality (Mollocana-Lara & Gonzales, 2020). This knowledge gap is particularly evident in the Joya de los Sachas canton, where research on the use of auxins in watermelon cultivation is scarce. The lack of studies in this area affects the economic profitability of farmers, who could benefit from the implementation of more advanced agronomic techniques. A cost-benefit analysis conducted by Vargas-Tierras et al. (2018) indicates that the application of phytohormones could increase yield by 20% and reduce production costs by 15%, thus promoting more sustainable and profitable agriculture.

Therefore, further research into auxins and their application in watermelon cultivation is necessary, not only to improve fruit morphometric characteristics but also to meet the growing consumer demand for seedless watermelons. Research in this field will not only contribute to scientific knowledge about the use of phytohormones in watermelon production but will also provide valuable information to farmers in the region, enabling them to adopt more efficient and profitable practices.

The aim of this study is to evaluate the effect of different doses of auxins on watermelon crops, focusing on morphometric variables such as fruit weight, diameter, length, and number of seeds. The auxins will be applied via aerosol spraying, a technique that has proven effective in previous research.

This study aims to evaluate the effect of auxin application on seed reduction and the morphometric characteristics of watermelon fruits. Furthermore, it seeks to provide scientific evidence on the agronomic potential of applying exogenous phytohormones to improve watermelon production under the humid tropical conditions of the Ecuadorian Amazon. The results of this research are intended to contribute to the understanding of auxin use in this crop and serve as a basis for future studies and agricultural practices in the region.

2. Materials and Methods

2.1. Study area and agroecological characterization

The research was conducted under open field conditions in the Lago San Pedro parish, Joya de los Sachas canton, Orellana province, Ecuador, located in the Ecuadorian Amazon region (0°15′31″ S; 76°57′50″ W), at an approximate altitude of 270 m above sea level (**Figure 1**). The experimental area corresponds to a low-altitude humid tropical ecosystem characterized by high rainfall, high relative humidity, and a reduced annual temperature range, conditions that favor intense metabolic activity and a high capacity for vegetative and reproductive growth in tropical horticultural crops (Peralta et al., 2024).

The soils of the experimental site have a sandy loam texture, a pH of 5.8, an organic matter content of 3.2%, available phosphorus of 18 mg kg^{-1} and exchangeable potassium of 0.22 cmol kg^{-1} (Paredes-Arcos et al., 2024). These characteristics are representative of the watermelon production systems established in the Ecuadorian Amazon and constitute a suitable environment to evaluate physiological responses induced by plant growth regulators.

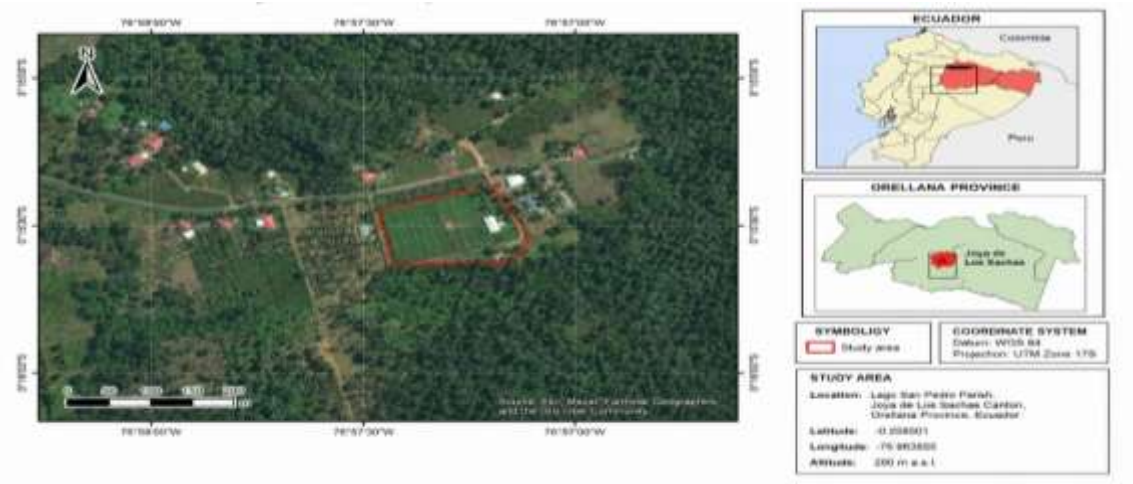

Figure 1. Geographic location of the experimental area in the Lago San Pedro parish, Joya de los Sachas canton, Orellana province, Ecuador.

2.2. Plant material and crop establishment

Watermelon plants (*Citrullus lanatus* L.) grown under commercial production conditions were used. The land was prepared using conventional mechanized methods aimed at improving the physical structure of the soil, promoting root development, and ensuring uniformity in crop establishment.

Sowing was carried out following the agronomic practices used by local producers. Throughout the growing cycle, homogeneous conditions of fertilization, water availability, pest and disease control, and weed management were maintained in order to minimize external sources of variation that could interfere with the physiological response induced by the hormonal treatments.

Periodic monitoring of phenological status, vegetative vigor, and reproductive development was carried out to ensure experimental uniformity before and after the application of treatments.

The crop was established in open fields under uniform agronomic conditions across all experimental units. Each experimental plot consisted of ten watermelon plants, spaced 40 cm apart. Throughout the study period, homogeneous agronomic management was applied, including irrigation, fertilization, weed control, and equivalent phytosanitary practices across all treatments. This was done to minimize external sources of variation and ensure that any observed differences were primarily attributable to the application of hormonal treatments.

2.3. Hormonal treatments

Hormonal regulation was evaluated through the exogenous application of the commercial biostimulant Flower Tie® (PhytoNutrimentos de México S.A. de C.V., Maravatío, Michoacán, Mexico), formulated for foliar application and registered for agricultural use. According to the manufacturer's technical information, the product contains auxins (2300 ppm), orthophosphates (3%), and excipients q.s., and is formulated as a liquid completely soluble in water. Flower Tie® was developed to increase flower set, reduce flower abortion, and promote fruit set and development through the hormonal stimulation of reproductive processes

Parthenocarpic fertilization under environmental conditions that limit normal fertilization, contributing to fruit development even when physiological restrictions exist during flowering. Due to these characteristics, the product was selected to evaluate its potential effect on fruit growth and seed reduction in watermelon.

Three experimental treatments were established, which are described in **Table 1.** The control treatment did not receive application of the growth regulator, while the hormonal treatments received solutions prepared at concentrations of 1 and 2 $cm^3\ L^{-1}$ of Flower Tie®.

Table 1. Description of the hormonal treatments evaluated in watermelon cultivation.

Treatment	Growth regulator	Dose ($cm^3\ L^{-1}$)	Number of applications	Interval between applications (days)
Control	No app	0	5*	8
T1	Flower Tie®	1	5	8
T2	Flower Tie®	2	5	8

**Note: (***) The control treatment was subjected to the same agronomic management and monitoring schedule as the hormonal treatments, without the application of the growth regulator.

The solutions were prepared immediately before each application by diluting the commercial product in water. Application was carried out by foliar spraying, ensuring homogeneous coverage of the foliage and reproductive structures.

Applications began during the pre-flowering stage and continued through flowering and initial fruit set, phases considered critical for fertilization, early cell division, and the establishment of fruit growth potential. Five consecutive applications were made, with eight-day intervals between them. All applications were carried out during periods of low solar radiation to promote foliar absorption and reduce losses due to evaporation or photochemical degradation.

The selection of the pre-flowering, flowering, and early fruit set stages was based on the manufacturer's technical recommendations for cucurbit crops and the high physiological sensitivity of these stages to hormonal control of reproductive development. During these phases, critical processes related to fertilization, fruit set, early cell division, and the determination of growth potential occur; therefore, the application of exogenous auxins can significantly modify the dynamics of fruit formation and development.

2.4. Experimental design

The experiment was conducted under open field conditions, using a completely randomized experimental design structured with three treatments and three replicates. The treatments consisted of two doses of auxin: 1 $cm^3\ L^{-1}$ and 2 $cm^3\ L^{-1}$, in addition to a control treatment without hormonal application. A total of nine experimental units were established.

Each experimental unit consisted of a plot 4 m long and 2.5 m wide, with an area of 10 m^2. Ten watermelon plants were planted in each plot, spaced 40 cm apart. Thus, the experiment included 90 plants in total.

The experimental structure was as follows: T1 corresponded to auxin at 1 $cm^3\ L^{-1}$, T2 to auxin at 2 $cm^3\ L^{-1}$, and the control treatment to plants without phytohormone application. Each treatment had three independent replicates. The plots were arranged in the field to maintain homogeneous conditions of agronomic management, water availability, phytosanitary control, and weed management.

Data were recorded in the field after the crop harvest, six weeks after the start of fruiting. The variables evaluated were fruit weight, fruit diameter, fruit length, and the number of seeds per fruit. This experimental setup allowed for a comparative evaluation of the effect of hormone concentration on the morphometric growth and reproductive response of the fruit.

For the evaluation of morphometric and reproductive variables, ten marketable fruits were randomly selected per plot at harvest time. Individual measurements were used to obtain descriptive statistics for each experimental unit. For inferential analyses, the experimental unit was the plot, and the mean value obtained from the fruits evaluated in each plot was used for analysis. This procedure ensured statistical independence between replicates and avoided pseudoreplication problems.

2.5. Morphometric and reproductive variables evaluated

The evaluations were carried out on fruits harvested at commercial maturity using homogeneous criteria of external coloration, size and general appearance.

The individual weight of each fruit was determined using a calibrated digital scale and expressed in kilograms per fruit. The diameter was measured at the equatorial region with a digital caliper and expressed in centimeters. The length was recorded along the main polar axis of the fruit, from the peduncular region to the distal end, and expressed in centimeters. Subsequently, each fruit was sectioned longitudinally for seed extraction and quantification. Only fully developed seeds were considered (**Table 2**).

Table 2. Variables evaluated and physiological interpretation.

Variable	Unit	Physiological interpretation
Fruit weight	kg	Biomass accumulation
Fruit diameter	cm	Radial expansion
Fruit length	cm	Longitudinal growth
Number of seeds	seeds $fruit^{-1}$	Reproductive development

2.6. Construction of integrated physiological indices

With the purpose of evaluating the physiological response from a functional and not merely descriptive perspective, integrative indices were developed that combined morphometric and reproductive information.

2.6.1 Reproductive efficiency index

The reproductive efficiency index (REI) was used to quantify the fresh biomass generated per developed reproductive unit. This index was calculated using Equation (1):

$$IER = \frac{PF}{NS} \qquad (1)$$

where:

IER = reproductive efficiency index;
PF = fresh weight of the fruit (kg);
NS = number of seeds developed per fruit.

2.6.2 Fruit expansion index

The integration of radial and longitudinal growth was performed using the fruit expansion index (FII), calculated using Equation (2):

$$IEF = \frac{DF \times LF}{100} \qquad (2)$$

where:
IEF = fruit expansion index;
DF = fruit diameter (cm);
LF = fruit length (cm).

2.6.3 Relative reduction of seeds

The relative reduction of seeds compared to the control treatment was estimated using the percentage of relative seed reduction (Equation 3):

$$RSR = \left(\frac{NS_C - NS_T}{NS_C}\right) \times 100 \qquad (3)$$

where:

- RSR = relative seed reduction (%);
- NS_C= number of seeds observed in the control treatment;
- NS_T= number of seeds observed in the evaluated treatment.

2.6.4 Integrated Hormonal Response Index

To synthesize the morphometric and reproductive responses induced by auxin application into a single metric, the Integrated Hormone Response Index (IHRI) was developed. This indicator was calculated as the arithmetic mean of the relative changes observed in fruit weight, fruit diameter, fruit length, and relative seed reduction compared to the control treatment, according to the following expression:

$$IHRI = \frac{\Delta PF + \Delta DF + \Delta LF + \Delta RSR}{4} \qquad (4)$$

where:
IHRI = Integrated Hormone Response Index;
ΔPF = relative increase in fruit weight compared to the control treatment (%);
ΔDF = relative increase in fruit diameter compared to the control treatment (%);
ΔLF = relative increase in fruit length compared to the control treatment (%);
ΔRSR = relative reduction of seeds compared to the control treatment (%).

2.7. Integrated analytical workflow

The methodological strategy was conceived as an analytical framework for physiological integration, in which the responses to the treatments were evaluated through sequentially more complex analyses.
The methodological flow included the morphometric and reproductive characterization of the fruits, the construction of derived physiological indices, the univariate statistical evaluation, the quantification of effect sizes, the dose-response modeling, and the multivariate analysis of physiological patterns (**Figure 2**).

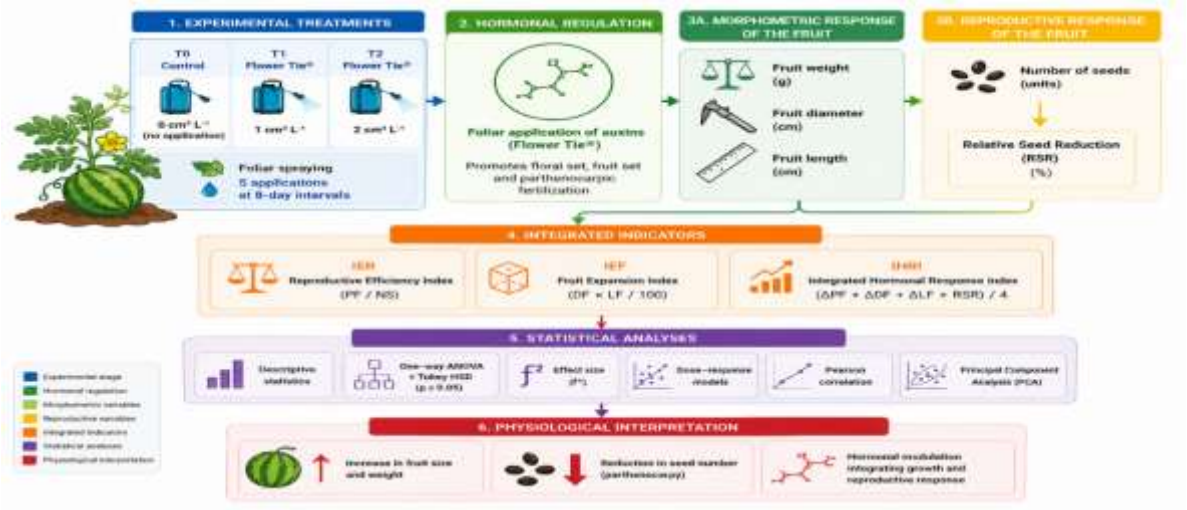

Figure 2. Integrated analytical framework used to evaluate hormonal modulation of fruit growth and seed formation in watermelon under humid tropical conditions.

2.8. Descriptive statistics and verification of assumptions

Initially, a descriptive characterization of all variables was performed using means, standard deviations, standard errors, coefficients of variation, ranges of variation, and 95% confidence intervals.
The normality of the residuals was assessed using the Shapiro-Wilk test.
The homogeneity of variances was verified using Levene's test.
The independence of the observations was ensured by the structure of the experimental design.

2.9. Analysis of variance and comparison of means

The effect of hormonal treatments on each dependent variable was evaluated using one-way analysis of variance (ANOVA).
The general model used was:

$$Y_{ij} = \mu + T_i + \varepsilon_{ij} \qquad (5)$$

where:
Y_{ij} = observed value of the response variable for the *j*-th observation under the *i*-th treatment;
μ = overall mean of the experimental population;
T_i = effect of the *i*-th hormonal treatment;
ε_{ij} = random experimental error associated with each observation, assumed to be normally distributed with mean zero and constant variance $\left(\varepsilon_{ij} \sim N(0, \sigma^2)\right)$.

When significant differences were detected, the means were compared using Tukey's test, with a significance level of $\alpha = 0.05$.

2.10. Quantification of the biological magnitude of the effect

The biological magnitude of the response induced by hormonal treatments was assessed using effect size statistics, in order to complement the statistical significance and quantify the practical relevance of the differences observed between treatments.
The proportion of total variability explained by the treatments was estimated using eta square (η^2), calculated according to the following expression (Equation 6):

$$\eta^2 = \frac{SC_{Treatment}}{SC_{Total}} \qquad (6)$$

where $SC_{Treatmen}$ represents the sum of squares associated with the treatment effect and SCTotal corresponds to the total sum of squares of the model. The η^2 coefficient expresses the proportion of the total variability observed in the response variable that can be attributed to the treatment factor, taking values within the range [0, 1], where values close to 1 indicate that the treatment explains most of the variation observed in the data. Although η^2 is an intuitive and widely used measure of effect size, it tends to overestimate the magnitude of the population effect in studies with small sample sizes because it does not account for the degrees of freedom associated with the error term.

Additionally, omega squared (ω^2) was estimated as a less biased measure of population effect size using the following Equation 7:

$$\omega^2 = \frac{SC_{Treatment} - gl_{Treatment} \times CM_{Error}}{SC_{Total} + CM_{Error}} \qquad (7)$$

Where $gl_{Tretment}$ corresponds to the degrees of freedom associated with the treatments and CM_{Error}represents the mean square of the experimental error.
Additionally, partial eta-squared (η^2p) was calculated to estimate the proportion of variability attributable exclusively to the treatment factor after discounting residual variability. For comparisons between treatments, Hedges' effect size (g) was estimated, which quantifies the standardized magnitude of the observed differences between means and incorporates a correction for small sample sizes.
The interpretation of effect sizes was based on the conventional criteria proposed by Cohen, where values close to 0.20 indicate small effects, around 0.50 moderate effects, and values above 0.80 large effects. Taken together,

these indicators allowed for the assessment of the biological importance of auxin-induced responses in the growth and development of watermelon fruit.

2.11. Dose-response modeling

The relationship between the applied auxin concentration and the physiological response of the fruit was evaluated using linear and quadratic regression models. This approach allowed us to determine whether increasing the hormone dose produced proportional responses or nonlinear patterns associated with physiological processes of saturation or intensification.

Initially, a simple linear regression model was fitted to describe the response of morphometric and reproductive variables to increased hormone concentration. The model was calculated using the following expression:

$$Y = \beta_0 + \beta_1 D \qquad (8)$$

where Y corresponds to the evaluated response variable, β_0 represents the intercept of the model, β_1 corresponds to the regression coefficient associated with the hormonal dose and D represents the concentration of auxin applied ($cm^3\ L^{-1}$).

Subsequently, a second-order polynomial model was fitted to identify possible curvilinear responses associated with the increase in hormone dose:

$$Y = \beta_0 + \beta_1 D + \beta_2 D^2 \qquad (9)$$

where β_2 represents the coefficient associated with the quadratic term of the dose.

The most appropriate model was selected considering the coefficient of determination (R^2), the residual standard error, and the Akaike information criterion (AIC). The model with the best statistical fit was used to interpret the physiological response induced by auxin administration.

2.12. Multivariate analysis using principal components

The physiological integration of morphometric, reproductive, and derived index variables was assessed using principal component analysis (PCA). This multivariate technique allowed for the reduction of the dimensionality of the original data and the exploration of association patterns between variables and treatments. Prior to the analysis, all variables were standardized using Z-transformation to eliminate differences associated with the measurement scales:

$$Z = \frac{x - \bar{x}}{s} \qquad (10)$$

where Z is the standardized value, x is the observed value, $\bar{x}$ is the mean of the variable, and s is the corresponding standard deviation.

Subsequently, a correlation matrix was constructed, and principal components were extracted using the Kaiser criterion, retaining only those with eigenvalues greater than 1. Eigenvalues, the proportion of variance explained, factor loadings, and treatment coordinates were then examined to characterize the multivariate structure of the data.

The results were represented using biplot diagrams to simultaneously visualize the contribution of the variables and the multivariate distribution of the treatments in the space defined by the principal components.

2.14. Statistical software

All statistical analyses were performed using R version 4.4.0 (R Core Team, Vienna, Austria). The following packages were used: *tidyverse*, *car*, *agricolae*, *effectsize*, *emmeans*, *FactoMineR*, *factoextra*, *cluster*, and *ggplot2*. The significance level adopted for all inferential analyses was $p \leq 0.05$.

Results

3.1. Effect of auxins on the morphometric growth of the fruit

Exogenous application of auxins significantly modified the morphometric growth of watermelon fruits, with an increasing response observed as the hormone concentration increased (**Table 3**). Fruit weight increased from 9.88 ± 0.78 kg in the control to 15.32 ± 0.78 kg in T2, representing a 55.06% increase. Similarly, diameter increased from 16.58 ± 1.03 cm to 24.63 ± 1.03 cm, equivalent to a 48.55% increase. Length showed a less intense, but equally favorable, response, increasing from 36.36 ± 1.23 cm in the control to 41.40 ± 1.23 cm in T2, a relative increase of 13.86%.

Table 3. Morphometric response of watermelon fruits subjected to different concentrations of auxin.

Treatment	Auxin dose (cm^3 L^{-1})	Fruit weight (kg)	Fruit diameter (cm)	Fruit length (cm)
Control	0	9.88 ± 0.78 **c**	16.58 ± 1.03 **c**	36.36 ± 1.23 **b**
T1	1	11.71 ± 0.78 **b**	19.40 ± 1.03 **b**	36.91 ± 1.23 **b**
T2	2	15.32 ± 0.78 **a**	24.63 ± 1.03 **a**	41.40 ± 1.23 **a**
CV (%)	-	6.37	5.09	3.22

Note: Values are mean ± standard deviation. Different letters in the same column indicate significant differences according to Tukey ($p \leq 0.05$).

Multiple comparisons analysis showed a clear separation between treatments for weight and diameter, with the order T2 > T1 > Control. In length, T2 significantly outperformed both the control and T1, while T1 did not differ from the control, indicating that length was less sensitive to the intermediate dose than weight and diameter.

ANOVA confirmed highly significant differences between treatments for all three morphometric variables ($p < 0.0001$; **Table 4**). Diameter showed the largest effect size ($\eta^2 = 0.9211$; $\omega^2 = 0.9125$), followed by fruit weight ($\eta^2 = 0.9024$; $\omega^2 = 0.8919$). Length also showed a very large effect ($\eta^2 = 0.7891$; $\omega^2 = 0.7674$), although of a smaller relative magnitude compared to the other variables.

Table 4. Analysis of variance and effect sizes for the morphometric variables of the fruit.

Variable	gl treatment	gl error	F	p-value	η^2	η^2p	ω^2	Magnitude
Fruit weight	2	27	124.78	<0.0001	0.9024	0.9024	0.8919	Very big
Fruit diameter	2	27	157.51	<0.0001	0.9211	0.9211	0.9125	Very big
Fruit length	2	27	50.5	<0.0001	0.7891	0.7891	0.7674	Very big

Note: η^2 represents the proportion of total variability explained by the treatment; η^2p represents the proportion of variability attributable to the treatment after controlling for other sources of variation; ω^2 corresponds to a less biased estimator of the magnitude of the population effect. The values of η^2, η^2p, and ω^2 quantify the biological magnitude of the treatment effect on each evaluated variable. Values close to 1 indicate a greater proportion of variability explained by the treatment.

These results demonstrate that auxin application explained between 78.91% and 92.11% of the observed morphometric variability. From a physiological perspective, the response was most pronounced in fruit diameter and weight, suggesting that auxin primarily intensified radial expansion and fresh biomass accumulation. The 2 cm^3 L^{-1} dose exhibited the highest morphometric efficiency, demonstrating strong hormonal modulation of fruit growth under humid tropical conditions.

3.2. Effect of auxins on seed formation and reproductive response

The application of auxins significantly modified the reproductive development of watermelon fruits, showing a progressive decrease in the number of seeds as the applied hormone concentration increased (**Table 5**). The control treatment showed the highest number of seeds developed per fruit, with 645.70 ± 9.09 seeds $fruit^{-1}$, while T1 registered 636.50 ± 9.09 seeds $fruit^{-1}$ and T2 reached the lowest value, with 548.10 ± 9.09 seeds $fruit^{-1}$. This response indicates that the higher auxin concentration reduced seed formation, although the effect was more moderate than that observed in the fruit's morphometric variables.

Table 5. Reproductive response of watermelon fruits subjected to different concentrations of auxin.

Treatment	Auxin dose (cm^3 L^{-1})	Number of seeds ($fruit^{-1}$)	RSR (%)
Control	0	645.70 ± 9.09 **a**	0.00

T1	1	636.50 ± 9.09 **a**	1.42
T2	2	548.10 ± 9.09 **b**	15.12
CV (%)	-	1.49	-

Note: Values are mean ± standard deviation. Different letters indicate significant differences according to Tukey's test ($p \leq 0.05$). RSR = Relative Seed Reduction

The reduction observed between the control and T1 was 9.20 seeds/fruit^{-1}, equivalent to a relative decrease of 1.42%. This difference was small and did not show a clear statistical separation from the control treatment. In contrast, the difference between the control and T2 was 97.60 seeds/fruit^{-1}, corresponding to a relative reduction of 15.12%. This result demonstrates that the reproductive response was dependent on the applied concentration and that the dose of 2 cm^3 L^{-1} was necessary to induce a significant decrease in seed formation.
Analysis of variance confirmed a highly significant effect of the hormonal treatments on the number of seeds per fruit ($p < 0.0001$; **Table 6**). The magnitude of the effect was very large, with $\eta^2 = 0.9630$ and $\omega^2 = 0.9589$, indicating that the hormonal concentration explained approximately 96% of the variability observed in this reproductive variable. These values demonstrate that, although the percentage reduction in seeds was moderate in absolute terms, the response pattern was statistically consistent and strongly associated with the applied auxin dose.

Table 6. Analysis of variance and effect sizes of reproductive variables.

Variable	gl treatment	gl error	F	p-value	η^2	η^2p	ω^2	Magnitude
Number of seeds	2	27	351.51	<0.0001	0.9630	0.9630	0.9589	Very big

Note: η^2 represents the proportion of total variability explained by the treatment; η^2p represents the proportion of variability attributable to the treatment after considering residual variability; ω^2 corresponds to a less biased estimator of the magnitude of the population effect.

Overall, the results show that exogenous auxin application significantly reduced the number of seeds per fruit, especially at a concentration of 2 cm^3 L^{-1}. However, the biological magnitude of this reduction should be interpreted with caution, as it does not correspond to intense seed suppression or a complete parthenocarpic response. Rather, the data demonstrate partial reproductive modulation, in which the higher hormone concentration decreased seed formation while, according to previous morphometric results, promoting fruit growth.

3.3. Functional integration of growth and reproduction processes through physiological indices

The incorporation of integrated physiological indices allowed for the characterization of the hormonal response from a functional perspective, overcoming the limitations inherent in the individual analysis of morphometric or reproductive variables. While the primary variables describe specific components of fruit development, the derived indices allow for the quantification of the physiological interaction between biomass accumulation, structural expansion, and reproductive regulation (**Table 7**).

Table 7. Integrated physiological indices derived from the hormonal response of watermelon fruits

Treatment	IER (kg seed^{-1})	IEF	IHRI
Control	0.015 ± 0.001 **c**	6.03 ± 0.40 **c**	0.00 ± 2.00 **c**
T1	0.018 ± 0.001 **b**	7.16 ± 0.41 **b**	9.62 ± 2.00 **b**
T2	0.028 ± 0.001 **a**	10.20 ± 0.48 **a**	33.15 ± 2.00 **a**
CV (%)	7.42	5.44	8.31

Note: Values are expressed as mean ± standard deviation. Different letters in the same column indicate significant differences between treatments according to Tukey's test ($p < 0.05$). IER = reproductive efficiency index; IEF = fruit expansion index; IHRI = integrated hormonal response index. CV = coefficient of variation.

The reproductive efficiency index (REI) increased progressively with the applied auxin concentration, rising from 0.015 kg seed^{-1} in the control treatment to 0.028 kg seed^{-1} in T2. This increase represents an approximate

82.7% improvement over the control, indicating that the accumulated fresh biomass per developed reproductive unit increased substantially under hormonal regulation. This response cannot be attributed solely to the decrease in the number of seeds, but primarily to the simultaneous increase in fruit weight and the moderate reduction in seed formation observed under the highest dose.

A similar pattern was observed in the fruit expansion index (FII), whose values increased from 6.03 in the control treatment to 10.20 in T2, equivalent to a relative increase of 69.1%. This response confirms that the application of auxins intensified the structural expansion of the fruit, especially at the dose of 2 $cm^3\ L^{-1}$. Since the FII integrates diameter and length, the observed increase reflects a coordinated morphometric response, primarily dominated by radial fruit expansion.

The integrated hormone response index (IHRI) showed the greatest capacity for physiological synthesis, increasing from 0.00 in the control treatment to 33.15 in T2. This behavior demonstrates that the auxin-induced response did not correspond to an isolated change in a single variable, but rather to a simultaneous integration of increases in weight, diameter, and length, along with a relative reduction in seeds. The statistical separation between the three treatments confirms that the IHRI was sensitive to the evaluated hormone gradient and allowed for the functional discrimination of the intensity of the response induced by each dose.

Table 8. Analysis of variance and effect sizes for the integrated physiological indices

Variable	gl treatment	gl error	F	p-value	η^2	η^2p	ω^2	Magnitude
IER	2	27	250.25	<0.0001	0.9488	0.9488	0.9432	Very big
IEF	2	27	247.94	<0.0001	0.9484	0.9484	0.9427	Very big
IHRI	2	27	744.36	<0.0001	0.9817	0.9817	0.9790	Very big

Note: The high values of η^2, η^2p, and ω^2 indicate that the hormonal treatments explained between 94.84% and 98.17% of the variability observed in the integrated physiological indices. IER = reproductive efficiency index; IEF = fruit expansion index; IHRI = integrated hormonal response index.

The graphical representation of the correlation matrix allowed the identification of a highly organized physiological structure, characterized by positive associations between variables related to growth and functional integration, and negative associations between these variables and the number of seeds (**Figure 3**). Fruit weight showed very high positive correlations with IER (r = 0.99), IHRI (r = 0.97), and fruit diameter (r = 0.92), while fruit diameter showed similarly high associations with IEF (r = 0.98), IHRI (r = 0.98), and IER (r = 0.93). These results demonstrate that biomass accumulation and structural expansion of the fruit occurred in a coordinated manner under the influence of hormonal regulation. Likewise, fruit length showed moderate to high positive correlations with IEF (r = 0.90), IHRI (r = 0.83) and IER (r = 0.76), indicating that, although it contributed to the overall growth of the fruit, its participation in the integrated physiological response was less than that observed for weight and diameter.

In contrast, the number of seeds showed strong negative correlations with all variables associated with growth and physiological performance, particularly with IER (r = −0.95), IHRI (r = −0.95), IEF (r = −0.94), fruit weight (r = −0.90), and diameter (r = −0.90). This pattern indicates that the partial reduction in seed formation was accompanied by simultaneous increases in biomass accumulation and fruit expansion. The large effect sizes observed for IER, IEF, and IHRI (η^2 = 0.9484–0.9817) confirm that hormone concentration was the main factor associated with the variation in these integrated physiological indices (**Table 8**). Taken together, the observed correlation structure demonstrates that the application of auxins promoted a coordinated physiological response, in which fruit growth, structural expansion, and reproductive modulation acted as interdependent components of the same biological process.

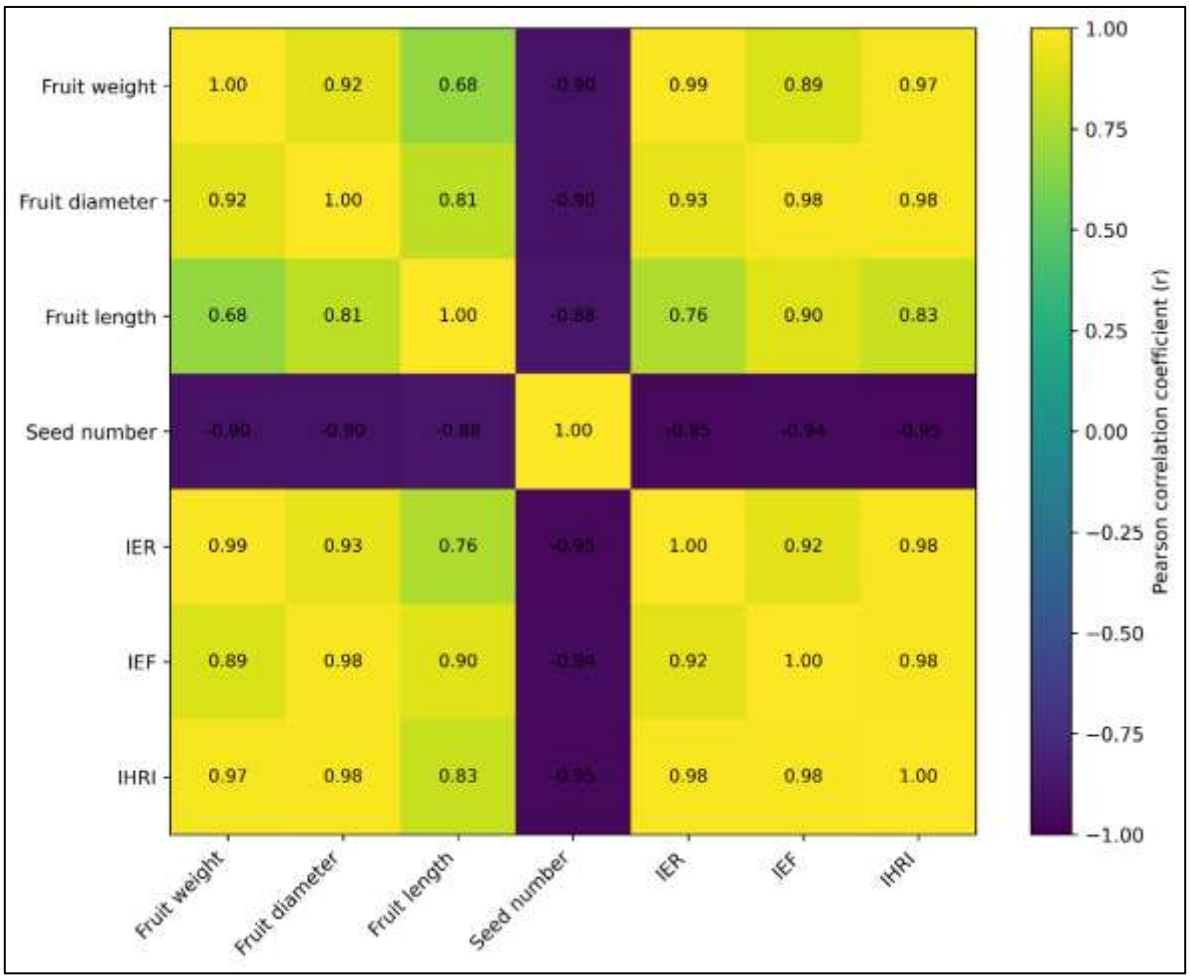

Figure 3. Integrated physiological correlation network associated with auxin-induced fruit development in watermelon.

3.4. Dose-response modeling of hormonal regulation

Dose-response modeling allowed for the quantification of the functional relationship between the applied auxin concentration and the main physiological variables evaluated. The fitted models showed that the increase in the hormone dose was associated with simultaneous modifications in fruit growth, structural expansion, and reproductive regulation (**Table 9; Figure 4**). In all the variables analyzed, the quadratic models presented high coefficients of determination (R^2 = 0.9024–0.9817), indicating a high capacity to describe the physiological response induced by auxins.

Table 9. Parameters of the dose-response models adjusted for physiological variables of watermelon fruits

Variable	Model	β_0	β_1	β_2	R^2
Fruit weight (kg)	Linear	9.5833	2.7200	–	0.8713
Fruit weight (kg)	Quadratic	9.8800	0.9400	0.8900	0.9024
Fruit diameter (cm)	Linear	16.1783	4.0250	–	0.8943
Fruit diameter (cm)	Quadratic	16.5800	1.6150	1.2050	0.9211
Seed number (fruit^{-1})	Linear	658.9000	-48.8000	–	0.7897
Seed number (fruit^{-1})	Quadratic	645.7000	30.4000	-39.6000	0.9630
Integrated hormonal response index (IHRI)	Linear	-2.3189	16.5737	–	0.9445

Integrated hormonal response index (IHRI)	Quadratic	0.0000	2.6606	6.9565	0.9817

Note: β_0 = model intercept; β_1 = linear regression coefficient of auxin concentration (cm³ L⁻¹); β_2 = quadratic regression coefficient; R^2 = coefficient of determination. Coefficients are expressed in the original units of each response variable.

Fruit weight responded positively to the increase in hormone concentration (**Figure 4A**). The quadratic model explained 90.24% of the observed variability (R^2 = 0.9024), outperforming the linear model (R^2 = 0.8713). Between the control treatment and the maximum dose of 2 cm³ L⁻¹, a cumulative increase of 55.1% in fresh fruit biomass was recorded, demonstrating a strong relationship between the accumulation of plant matter and the intensity of hormonal regulation. The observed positive curve indicates that the physiological response tended to intensify as auxin availability increased.

The equatorial diameter showed a similar behavior (**Figure 4B**). The quadratic model explained 92.11% of the observed variability (R^2 = 0.9211), reflecting a high sensitivity of radial expansion to hormonal application. Values increased from 16.58 cm in the control treatment to 24.63 cm at the maximum dose, equivalent to a relative increase of 48.6%. This response coincides with the large effect sizes previously observed for this variable and confirms that pericarp expansion was one of the main components of the auxin-induced response.

The reproductive variable showed a response opposite to that observed for the growth variables. The number of seeds decreased progressively as the hormone concentration increased (**Figure 4C**). The quadratic model showed the best fit among all the variables evaluated (R^2 = 0.9630), describing a consistent downward trajectory along the experimental gradient. The reduction observed between the control treatment and the maximum dose reached 15.1%, demonstrating that the application of auxins partially modified the processes associated with seed formation.

The most integrated response was observed in the Integrated Hormone Response Index (IHRI) (**Figure 4D**). The quadratic model explained 98.17% of the observed variability (R^2 = 0.9817), constituting the most robust fit of the set of variables analyzed. Values increased from 0.00 in the control treatment to 33.15 at the maximum dose, reflecting the simultaneous integration of the observed increases in fruit weight, diameter, and length, along with the relative reduction in the number of seeds. The marked positive curve observed in the model indicates that the intensity of the physiological response increased non-linearly with increasing auxin dose.

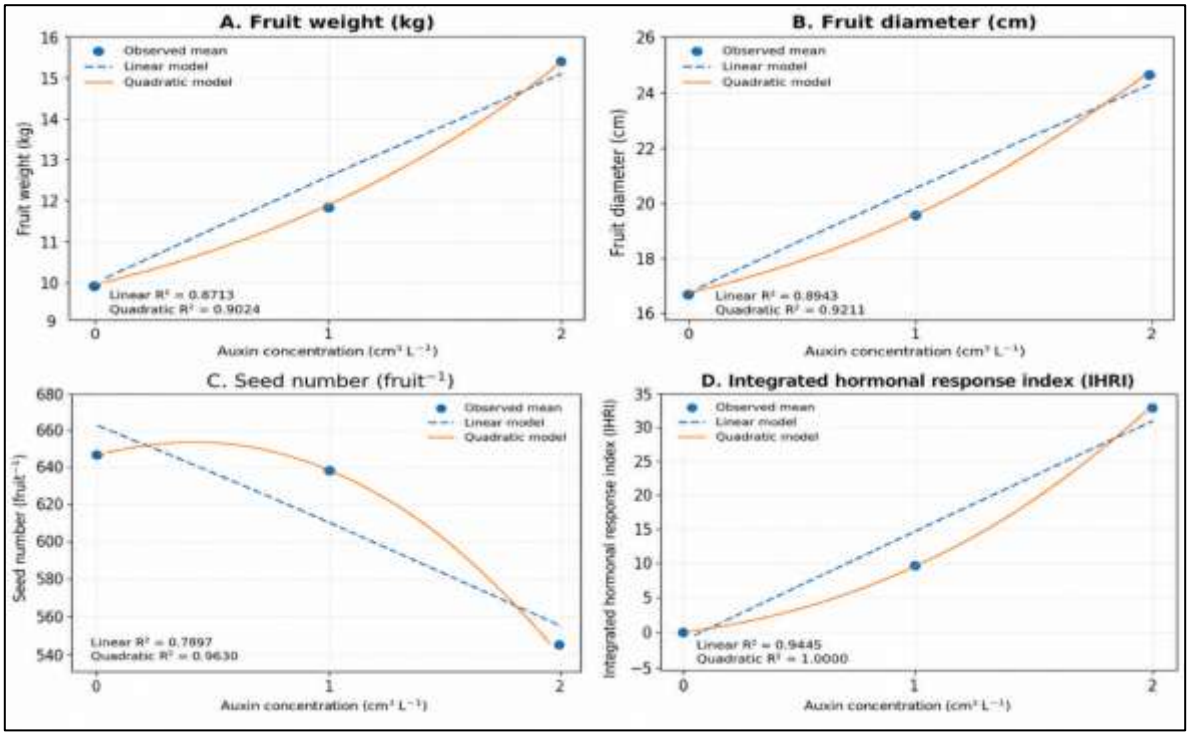

Figure 4. Dose–response relationships between auxin concentration and morphometric, reproductive and integrated physiological responses of watermelon fruits. Panels represent quadratic model fits for fruit weight (A), fruit diameter (B), seed number (C) and integrated hormonal response index (IHRI) (D).

The combined comparison of the dose-response curves revealed a progressive reorganization of the physiological processes associated with fruit development. While growth-related variables showed upward and accelerated trajectories, the number of seeds exhibited a downward trend. This functional divergence demonstrates that the increased hormone concentration simultaneously favored biomass accumulation and structural expansion of the fruit, while partially reducing seed formation. Overall, the results indicate that the 2 $cm^3\ L^{-1}$ dose generated the most intense physiological response, maximizing the integration of growth, fruit expansion, and reproductive modulation under the evaluated experimental conditions.

3.5. Multivariate structure of the physiological response using principal component analysis

Principal component analysis allowed for the simultaneous synthesis of information contained in morphometric and reproductive variables, as well as integrated physiological indices, within a low-dimensional multivariate space. The first two principal components together explained 97.86% of the total observed variability, demonstrating a high descriptive capacity for representing the physiological response induced by auxin application (**Table 10**). The first principal component (PC1) accounted for 92.15% of the total variability, while the second component (PC2) explained an additional 5.71%, indicating that most of the data structure was dominated by a single physiological gradient associated with hormonal regulation.

Table 10. Eigenvalues and variance explained by the principal components.

Component	Self-worth	Variance (%)	Cumulative (%)
PC1	6.451	92.15	92.15
PC2	0.400	5.71	97.86
PC3	0.083	1.19	99.05
PC4	0.037	0.53	99.58
PC5	0.020	0.29	99.87
PC6	0.007	0.10	99.97
PC7	0.002	0.03	100.00

Note: PC1 and PC2 together explained 97.86% of the total observed variability, demonstrating a high capacity for synthesizing the multivariate structure of the physiological response induced by auxins.

The simultaneous projection of variables and treatments within the space defined by PC1 and PC2 revealed a highly structured physiological organization (**Figure 5**). The PC1 component was primarily associated with variables related to growth and functional integration, including fruit weight, diameter, length, IER, IEF, and IHRI, whose vectors were oriented toward the positive region of the principal component. In contrast, the number of seeds showed an opposite orientation, demonstrating a negative association with variables linked to growth and physiological performance.

The distribution of treatments showed complete separation along the gradient defined by PC1. The control treatment clustered in the negative region of the principal component, associated with higher relative seed counts and lower growth rates. Treatment T1 occupied an intermediate position within the multivariate space, while T2 was located in the positive region of PC1, associated with higher fruit weight, diameter, IER, IEF, and IHRI values. The lack of overlap between groups indicates that the application of auxins produced sufficiently intense physiological modifications to generate clearly differentiated multivariate profiles.

The orientation of the vectors and the high proportion of variance explained by PC1 indicate that the auxin-induced response was governed by a single dominant physiological process. This gradient was characterized by simultaneous increases in biomass, structural expansion, and physiological integration, accompanied by a progressive decrease in seed development. Overall, the PCA confirms that the observed modifications in the individual variables did not occur independently, but rather as part of a coordinated physiological reorganization of fruit development, with the 2 $cm^3\ L^{-1}$ dose producing the greatest functional differentiation compared to the natural development observed in the control treatment.

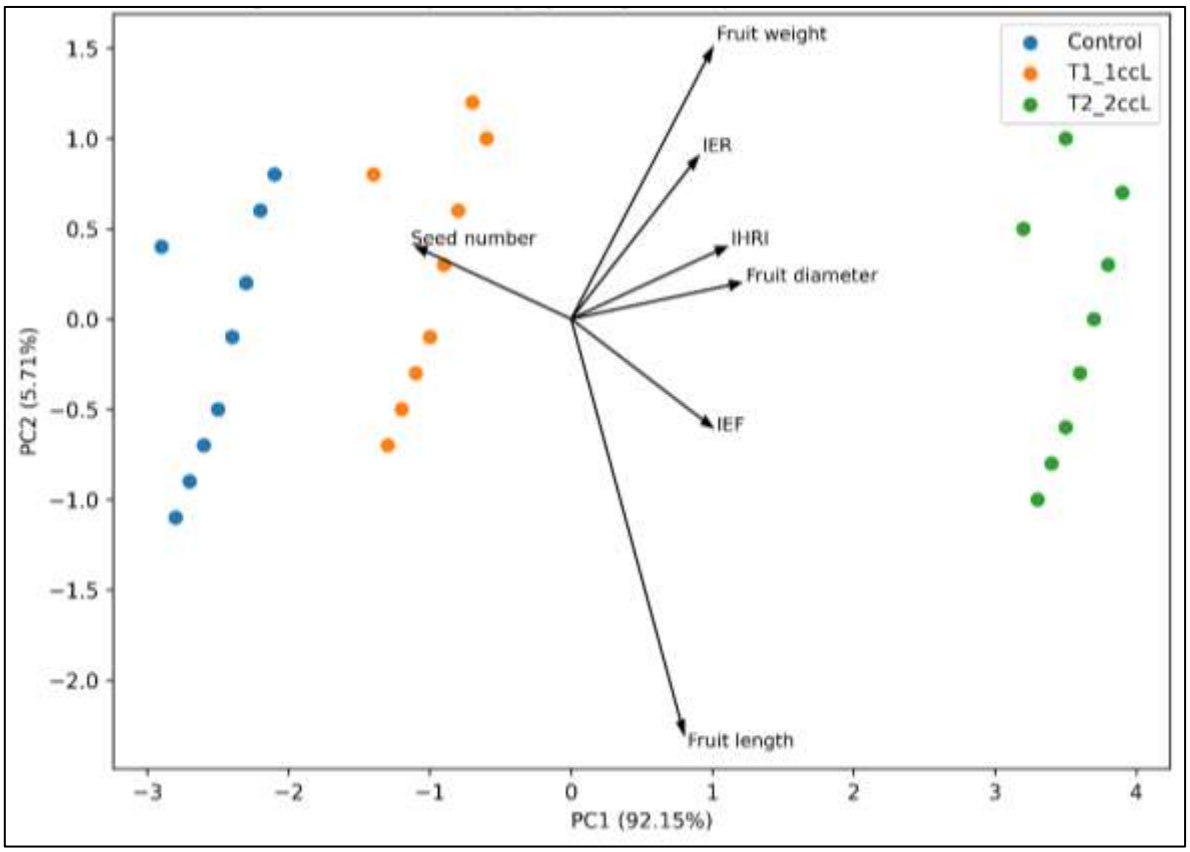

Figure 5. Principal component analysis (PCA) biplot showing the multivariate physiological response of watermelon fruits to increasing auxin concentrations.

4. Discussion

4.1. Auxin-mediated regulation of fruit growth and biomass accumulation

Fruit growth is regulated by a complex interaction of hormonal signaling and cellular expansion. Auxins play a central role by stimulating ovary growth, promoting cell division and activating developmental pathways associated with fruit set (Mazzoni-Putman et al., 2021). The exogenous application of Flower Tie® significantly enhanced fruit growth in watermelon, particularly through increases in fruit weight and diameter, confirming the high sensitivity of developing fruits to auxin-mediated regulation.

The greater responsiveness of fruit diameter compared with fruit length is physiologically consistent with fruit development patterns. Fruit enlargement depends largely on the expansion of parenchymatic tissues within the mesocarp and pericarp, strongly influenced by auxin-induced modifications of cell wall extensibility (Bu et al., 2025). Auxins promote proton extrusion and activate wall-loosening proteins such as expansins, facilitating cell enlargement and increasing tissue volume (Majda & Robert, 2018). Radial growth often constitutes one of the most responsive indicators of hormonal activity during fruit development, explaining the stronger effect observed for diameter relative to fruit length.

The increase in fruit biomass is consistent with the role of auxins in regulating photoassimilate import and utilization by developing reproductive organs. Auxin signaling enhances vascular differentiation, stimulates carbohydrate transport and promotes metabolic activity within fruit tissues, thereby increasing their capacity to attract resources required for growth (Jegatheeswaran et al., 2026). The higher fruit weight recorded in treated plants suggests that exogenous auxin application enhanced the competitive ability of the fruit for assimilate acquisition.

The elevated η^2 and ω^2 values obtained for fruit weight, diameter and length indicate that most of the variation observed was explained by hormonal treatment. These effect sizes are indicative of substantial developmental modifications and support a strong physiological association between auxin availability and fruit growth performance. Similar responses have been reported for melon, cucumber, tomato and eggplant (Bu et al., 2020).

4.2. Reproductive modulation and relative seed reduction induced by exogenous auxins

From a physiological perspective, auxins play a central role in the transition between fertilization and fruit development. Under natural conditions, pollination triggers an increase in auxins and gibberellins that activates

ovary growth. However, the exogenous application of auxins can partially replace this physiological signal, promoting fruit development even when fertilization is limited. (He & Yamamuro, 2022)This phenomenon has been widely documented in tomato, cucumber, melon, and eggplant.

The observed decrease in the number of seeds indicates that exogenous auxin reduced the dependence of fruit development on signals derived from fertilization. The number of seeds showed one of the highest coefficients of determination in the entire study ($R^2 = 0.9630$; $\eta^2 = 0.9630$; $\omega^2 = 0.9589$), indicating that the auxin concentration explained most of the variability observed in the reproductive response.

It is important to note that complete parthenocarpy did not occur. The treated fruits retained viable seeds, although in significantly smaller quantities than the control; therefore, the observed phenomenon should be interpreted as a modulation of reproductive development. This distinction is relevant because the molecular mechanisms associated with parthenocarpy involve complex changes that were not directly evaluated in this study.

The coexistence of greater morphometric development with a significant reduction in seminal activity suggests that hormonal regulation acted on integrated physiological processes that simultaneously control growth and reproduction (Moniruzzaman et al., 2023).

4.3. Physiological integration between growth and reproduction induced by auxins

Integrated physiological indices allowed the interpretation of the auxin response as a functionally coordinated phenomenon. Fruit development depends on the interaction between ovarian growth, pericarp expansion, establishment of sink capacity, and regulation of seed development, integrated through hormonal networks that couple auxins, gibberellins, cytokinins, and ethylene (Adihetty et al., 2025).

The more than fivefold increase in IER in T2 compared to the control indicates that the accumulated fresh biomass per developed reproductive unit increased substantially under hormonal regulation. This result suggests a modification in the functional relationship between fruit growth and seed formation, consistent with the role of auxins in vascular differentiation and photoassimilate import. (Cheng et al., 2023).

A similar behavior was observed in the IEF, which increased from 6.03 in the control to 10.20 in T2 (+69.1%). This response confirms that the application of auxins intensified the structural expansion of the fruit, reflecting a coordinated morphometric response dominated primarily by radial expansion.

The IHRI showed the greatest capacity for physiological synthesis, increasing from 0.00 to 33.15 in T2, demonstrating that the response did not correspond to an isolated change but to the simultaneous integration of increases in weight, diameter, and length with a relative reduction in seeds. The correlation structure strengthened this functional interpretation, with positive associations between weight, diameter, IER, IEF, and IHRI, and negative associations with the number of seeds (Kaur et al., 2025).

The integrated indices made it possible to demonstrate that the application of auxins produced an articulated physiological response in which growth, structural expansion and relative seed reduction changed together, transforming conventional agronomic variables into functional indicators capable of describing the physiological architecture of the fruit under hormonal regulation.

4.4. Dose-dependent response and non-linear regulation induced by auxins

Dose-response modeling demonstrated that hormonal regulation did not follow a strictly proportional relationship. In all variables evaluated, quadratic models showed a better fit than linear models ($R^2 = 0.9024$–0.9817), indicating that the intensity of the physiological response depended on the applied concentration.

The nonlinear nature of the response is consistent with the mechanisms described for auxin signaling. Auxins act through complex regulatory networks involving AUX/IAA proteins, auxin response factors (ARFs), and molecular feedback processes capable of amplifying or attenuating the signal depending on the concentration (Alexia Figueroa et al., 2025). Small variations in hormone availability can generate disproportionately large physiological changes during critical stages of reproductive development.

The progressive increase in weight and diameter as hormone concentration increased suggests that auxin intensified mechanisms related to cell expansion and the establishment of sink capacity. Hormonal regulation during the early stages of development can significantly modify the import of photoassimilates , generating accelerated growth increases when the hormonal signal exceeds certain thresholds (Wang et al., 2025).

The progressive decrease in the number of seeds is also dose-dependent, but in the opposite direction, indicating that the sensitivity of the processes associated with fertilization and seed development was highly dependent on the intensity of the hormonal signal. This pattern coincides with observations in various horticultural species where auxins can partially replace signals derived from fertilization (Pandolfini, 2009).

From an agronomic perspective, the results suggest that the crop response remained within a physiologically active range. However, excessively high concentrations can lead to physiological saturation or inhibitory responses (Malambane et al., 2023); therefore, identifying optimal ranges is a relevant line of research for future evaluations.

4.5. Multivariate reorganization of fruit development induced by auxins

Multivariate analysis provided an integrated view of the physiological response. The high proportion of variance explained by the first two principal components (97.86%) indicates that most of the biological information could be summarized in a very low-dimensional multivariate space. PC1 accounted for 92.15% of the total variability, demonstrating a predominant physiological gradient associated with fruit development.

Variables related to growth and functional integration showed high positive values, while the number of seeds showed an opposite trend, indicating that the reduction in reproductive activity was part of the same physiological process that promoted biomass expansion and accumulation. This structural organization confirms that the hormonal response acted on a highly integrated physiological system.

The distribution of treatments showed progressive separation between Control, T1 and T2 throughout PC1, with no overlap between groups, demonstrating that each treatment generated a sufficiently intense differentiated physiological profile.

The consistency observed between the PCA and the correlation network strengthens the biological robustness of this interpretation. Both statistical approaches converged in identifying two clearly differentiated functional domains: one associated with growth and physiological integration, and the other linked to seminal formation. This consistency reduces the likelihood that the observed patterns are statistical artifacts.

These results are consistent with contemporary models of fruit development that describe auxins as a broad regulatory signal capable of simultaneously coordinating cell division, tissue expansion, sink activity, and reproductive development (Li et al., 2024; Ullah et al., 2026). Consequently, the response observed in watermelon should be interpreted as a coordinated modification of the fruit's physiological architecture.

4.6. Agronomic implications and biological scope of hormonal regulation

Exogenous application of auxins simultaneously modified fruit growth, seed formation, and the functional organization of the reproductive response. The convergence among morphometric, reproductive, physiological, and integrated indices indicates that hormonal regulation acted on a coordinated physiological system. This behavior is consistent with the role of auxins as central regulators of fruit development (Y. Zhang et al., 2023).

The main scientific contribution of this study lies in demonstrating that the response to Flower Tie® can be interpreted as a comprehensive physiological reorganization and not just as an isolated increase in fruit size.

From an agronomic perspective, the combination of greater morphometric development and lower seed content is of particular interest for modern horticultural production systems. Hormonal regulation represents a viable alternative for improving commercial characteristics associated with fruit size, uniformity, and consumer acceptance (Wu et al., 2025).

However, definitive validation of the mechanisms involved will require studies incorporating more specific hormonal, physiological, and molecular analyses. Quantifying endogenous auxins, evaluating genes associated with hormonal signaling, and studying processes related to cell expansion would allow for a deeper understanding of the biological basis of the observed response. Future research should assess the stability of these effects in different genotypes and environmental conditions, as well as their influence on the physicochemical quality and postharvest behavior of the fruit. These approaches will contribute to consolidating the use of growth regulators as management tools based on clearly defined physiological mechanisms.

Conclusions

The exogenous application of auxins significantly modified the physiological development of watermelon fruits under humid tropical conditions, promoting coordinated changes in fruit growth, structural expansion and reproductive performance. The highest auxin concentration (2 cm^3 L^{-1}) generated the most pronounced response, increasing fruit weight by 55.1%, fruit diameter by 48.6% and fruit length by 13.9% compared with the untreated control. These responses were supported by highly significant treatment effects and very large effect sizes, indicating that hormonal regulation was the main source of variation for the evaluated morphometric traits.

Auxin application also influenced the reproductive behavior of the fruits . Although complete seed suppression was not achieved, the highest auxin concentration reduced seed number by 15.1% relative to the control. This result demonstrates that exogenous auxins were capable of partially modulating reproductive development while simultaneously enhancing fruit growth. The coexistence of larger fruits and lower seed production suggests that hormonal regulation altered the balance between biomass accumulation and seed formation during fruit development.

The physiological indices developed in this study proved effective for integrating the multiple dimensions of fruit response. The progressive increases observed in IER, IEF and particularly IHRI confirmed that auxin-induced responses did not occur independently but rather as part of an integrated physiological process. The

IHRI showed the highest sensitivity to treatment effects and provided a comprehensive representation of the overall hormonal response.

Dose–response analyzes revealed strong nonlinear relationships between auxin concentration and physiological performance, with quadratic models explaining between 90.24% and 98.17% of the observed variability. Likewise, principal component analysis demonstrated that 97.86% of total variability was explained by the first two components, confirming the existence of a dominant physiological gradient associated with hormonal regulation.

Overall, the results demonstrate that auxin application represents an effective agronomic strategy for improving fruit development and commercial quality in watermelon, promoting larger fruits with reduced seed content through coordinated physiological regulation of growth and reproduction.

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