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Article

Glucokinins promote the early development of *Capsicum chinense* (Jacq.)

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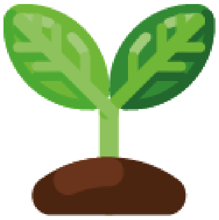
Abstract

apsicum chinense (Jacq.) has great economic importance, so it is a natural candidate for its implementation in protected agriculture (PA), but it has several challenges, the phenological stages and their adequate markers are not well defined, limiting the analysis of crop optimization. On the other hand, glucokinins have been shown to promote the early development of *in vitro* germination models. This study aimed to evaluate the effect of an animal glucokinin on the early development of *Capsicum chinense* (Jacq). The experiments were conducted in Tuxtepec, Oaxaca, 2016-2020, batches of 360 seeds per treatment (20 seeds x triplicate x six independent experiments) were exposed to glucokinin of animal origin, glucose, and Gao+glucose. Morphology parameters and growth rate were evaluated at each stage. The treatment with glucose and the combination delay germination ($p\geq 0.05$) but do not affect phenotype. Apparently, none affected the emergence ($p\geq 0.05$). There was a reduction in the overall time required for establishment ($p\leq 0.05$), the treatment with animal glucokinin decreased by 30%, glucose by 26%, and the combination by 26.3%. Treatment with animal glucokinin increased radicle length and lateral root number (p# 0.05 for all), whereas the hypocotyl length in the treatments is greater than the control. It is suggested that the application of animal glucokinin could be useful to optimize the crops of habanero chilis in PA, favoring development and reducing the time spent in the production modules.

Keywords:

conditioning, earliness, protected agriculture, seeds.



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Introduction

Protected agriculture (PA) allows for better management of water, spaces, and resources and protects crops from direct pest attack. However, the areas cannot be extensive due to the high cost of materials and inputs. To optimize the system, it is proposed to select crops with high profitability, use certified seeds, optimize irrigation, fertilize adequately, and use growth regulators that favor crop development and protect it from biotic and abiotic stress (Badji *et al*., 2022; Hernández-López, 2024).

Among the ideal vegetables for incorporation into PA is *Capsicum chinense* (Jacq.), habanero chili, which is a very profitable crop (between \$65.00 and \$130.00 MN kg^{-1}; SIAP, 2022); nevertheless, it still presents challenges to overcome, such as: i) the high cost of seed (\$5 400.00 MN per pound in INIFAP varieties) (Hernández-López *et al*., 2018); ii) loss of viability during storage (INIFAP guarantees germination greater than 80% in the seeds it sells for only three weeks) and iii) due to the problem of loss of viability, 2 or 3 seeds should be sown per space and the less developed ones should be sacrificed (Garruña-Hernández *et al*., 2014; Bissoli *et al*., 2022).

It should be noted that there is no consensus characterization on the phenological stages and the markers of each one, nor the time needed to reach them under standard study conditions (ISTA requirements), which prevents determining with certainty the effect of hormones, nutrients, or stress treatments on the optimization of the crop in PA.

The administration of biostimulants (BS) favors: a) the efficient use of nutrients; b) tolerance to abiotic stress; c) the quality of the fruits and d) the availability of nutrients in the rhizosphere (García-García, 2020). In this sense, glucokinins (Glk) are a family of insulin-related proteins that affect the regulation of carbohydrate metabolism in both animals (Gao) and plants (Gpo) (Hernández-López, 2024; Laguna-Hernández *et al*., 2017). They were first described by Eyster and Ellis (1924); the first studies of the effect of Glk were conducted on corn seedlings, where it was observed that they stimulate the growth of roots and coleoptile through a more efficient use of endosperm reserves. Azevedo *et al*. (2006) attributed a role in the hydrolysis of starch and its conversion to hexoses (glucose) to Glk.

They are also known to stimulate the conversion of fats to carbohydrates in squash and sunflower seeds (Goodman and Davis, 1993) and to stimulate cell growth in germinated corn embryos (Sánchez de Jiménez *et al*., 1999); in addition, Oliveira *et al*. (2004) found an increase in bean seedling size, whereas Avila-Alejandre *et al*. (2013) observed an increase in the expression of genes related to germination and the cell cycle in corn embryos; this effect was accompanied by greater growth of the radicle, with the participation of the protein kinase target of rapamycin (TOR), which was evidenced by the reversal of the effects after the application of rapamycin; Pascual-Morales *et al*. (2012) reported an increase in the growth of root hairs of *Arabidopsis* that was insulin-dose dependent.

Based on the above, it is suggested that Gao could accelerate the early development of *Capsicum chinense* (Jacq.) by promoting the root system. Therefore, this work aimed to evaluate the effect of a glucokinin of animal origin (Gao) on germination, emergence, and establishment (early development). In order to discriminate whether this stimulus has to do with a mitogenic activity related to the insulin receptor or the simple availability of glucose, glucose and the combination of glucose and Gao were used as a control.

Materials and methods

The experiments on the early development of *Capsicum chinense* (Jacq.) were carried out at the Chemical-Biological Laboratory of the University of Papaloapan-Tuxtepec and at the Labiott facilities, in Tuxtepec Oaxaca, from 2016 to 2020.

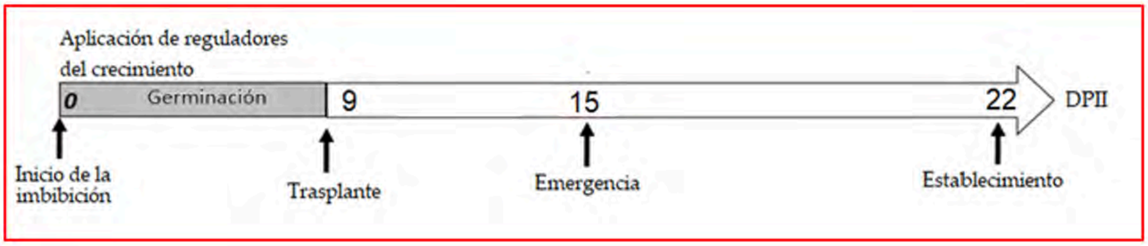
Biological material

The seeds used were mature seeds of *Capsicum chinense* (Jacq.), variety Jaguar, from the Las Huastecas Experimental Field of INIFAP in Tampico, Tamaulipas, Mexico, which were sown during the production cycle from December 2015 to February 2016. Once in the laboratory, sub-batches of 300 mg of seeds were separated and stored at 25 °C.

Early development kinetics

The effect of Glks on *Capsicum chinense* (Jacq.) was assessed in three stages of early development: germination, emergence, and establishment. In total, development was evaluated for 22 days for each experiment (Figure 1), as reported by Hernández-López *et al*. (2018).

Figure 1. Relevant dates of the development evaluation system (Hernández-López *et al*., 2018).



Germination trials were performed according to Hernández-López *et al*. (2018); batches of 20 seeds were exposed to 5 ml of: 1) Gao 0.063 µM (of bovine insulin; Sigma-Aldrich, Mexico cat. I5500) according to Ávila-Alejandre *et al*. (2013); 2) glucose 55 mM; 1%, according to Zhu *et al*. (2009) (JT Baker, USA); 3) the combination of Gao (0.063 µM)/glucose (55 mM) (Gao+glucose) and 4) distilled water as a control.

The seeds were incubated at 28 °C for nueve days with a photoperiod of 12 h light and 12 h dark. There were six independent replications in triplicate, 360 seeds per treatment. The number of germinated seeds was verified daily until the ninth day after the start of imbibition (9 DASI) according to Hernández-López *et al*. (2018). The inclusion criterion was that the protruding root was 2 mm long. The data obtained were used to calculate the cumulative germination (CG), expressed as a percentage, using the following equation: CG= (DSP/n)*100. Where: DSP is the daily number of seeds with protruding root; n is the number of seeds/replication.

The maximum observed cumulative germination (oCG$_{max}$) was established as the percentage of germination reached at 9 DASI, the inferred germination time 90 (iGT90) was calculated using PROBIT regression. From 9 DASI, all seeds (germinated or not) were transplanted as described in Hernández-López *et al*. (2018) to polystyrene pots with 5 g of Miracle-Gro potting substrate (The Scottslawn Company, Ohio USA) and were irrigated daily, and the emergence was monitored from 10 to 19 DASI or establishment from 14 DASI.

The inclusion criterion for emergence was the exit of the cotyledons above the substrate; for establishment, it was the appearance of true leaves of more than 3 mm in length. For both, the data were expressed as a percentage. For cumulative emergence (CE), the equation used was: CE= (DSE/n)*100; the cumulative establishment (CEst) was calculated with: CEst= (EstS/n)*100. Where: DSE is the daily number of seedlings with cotyledons emerged, EstS is the daily number of seedlings with true leaves and in both, n is the number of seeds used/replication.

The maximum observed emergence (CE$_{max}$) and the maximum observed establishment (CEst$_{max}$) were obtained when the number of seedlings with the inclusion criterion no longer changed in within two days of observation. The inferred emergence time 90 (iET90) and the inferred establishment time 90 (iEstT90) were also calculated using PROBIT regression.

Finally, at 22 DASI, the effect of the treatments on the phenotype of chili seedlings, expressed as the average length of the main root and the hypocotyl measured in mm, and the average number of lateral roots in each treatment were analyzed.

Dormancy time was defined as the day on which the first seed or seedling met the inclusion criteria. In each stage, the speed was calculated using least squares regression (first derivative) and was expressed as number (N°) of individuals meeting the criterion/day. Additionally, from these regressions, the time at which 50% of the population reached germination (GT50), emergence (ET50), or establishment (EstT50) was calculated.

Finally, for each stage, the rate of induction or inhibition of the treatments compared to the control was calculated. With the following formulas: RtInh= (t-E) x 100 or RtInd= (E-t) x100- E E. Where: RtInh is the inhibition rate; RtInd is the induction rate; t is the value of the maximum percentage of germination, emergence or establishment and E corresponds to the maximum percentage of germination, emergence or establishment with the inducers.

Statistical analysis

The experimental design was completely randomized. Batches of 360 seeds per treatment (20 seeds x triplicate x 6 independent experiments), the results were transformed into percentages and significant differences were determined by one-way Anova, comparing the means with the control through Tukey's test ($p \leq 0.05$). Regression was performed with PROBIT for the inferred times following the methodology reported by Hernández-López *et al*. (2018). These analyses were performed using the Minitab$^{®}$ software (Minitab Inc. 2007) version 15 for Windows, State College, Pennsylvania, USA. The plots were obtained with the Office Excel 2016 program (ver. 1611).

Results and discussion

Germination was the first stage analyzed (Figure 2A). No treatment favored the exit from dormancy ($p > 0.05$); on average, the first protrusion occurred around 5 DASI (Table 1). Figure 2 A showed that, although the percentages of CG did not show significant differences ($p > 0.05$), they did show the following trend: control> Gao> glucose> combination (Gao+glucose); that is, it was observed that all treatments tend to delay germination. At 9 DASI, only glucose significantly decreased ($p \leq 0.05$) oCG_{max} compared to the control.

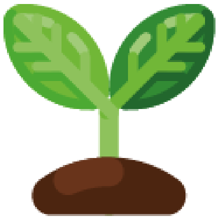


Figure 2. Early development response of *C. chinense* Jacq. The effect of Gao, glucose and the combination of Gao+glucose on three stages of early development of habanero chili is shown, the criteria established in each stage are shown. Different letters indicate significant differences between treatments (Tukey≤ 0.05).

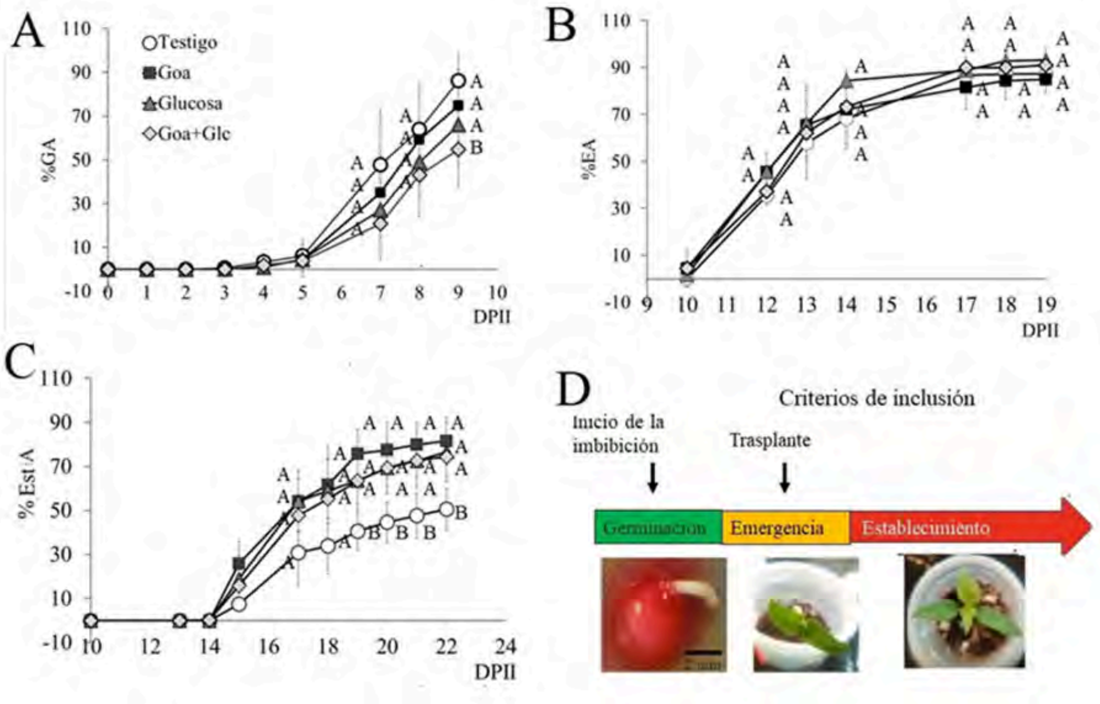


Table 1. Physiological parameters in the germination of samples of *C. chinense* (Jacq.) treated with the control, Gao, glucose and the combination.

Treatment	Dormancy (days)	Germination (0-9 DASI)			
		oCG$_{max}$ (%)†	GT$_{50}$ ††	Spe†††	RtInh (%)
Control	5 ±1.6^{A}	86 ±12.6^{A}	7.5 ±1.7^{A}	3.32 ±0.8^{A}	0
Gao	5 ±1.2^{A}	74.7 ±16^{A}	8.77 ±3^{A}	3.08 ±0.78^{A}	15.13
Glucose	5.8 ±1.36^{A}	65.9 ±17.4^{A}	11.7 ±4^{A}	2.61 ±0.74^{A}	30.5
Gao/Glu	5.6 ±1.3^{A}	54.7 ±18^{B}	10 ±3.3^{A}	2.2 ±0.72^{A}	57.22

† = maximum observed percentage of protruded seeds; †† = day after the start of imbibition (DASI) where 50% of the population has met the exclusion criteria; ††† = speed, expressed as number individuals/day. Different letters indicate significant differences between treatments (Tukey≤ 0.05).

Additionally, the inhibition rate of the effectors in comparison to the control was calculated. Gao had an inhibition of 15.7%, glucose 30.7%, and the Gao+glucose combination was 57.22%, the latter seems to show an additive effect (Table 1).

The inhibiting effect of glucose was previously observed by Dekkers *et al*. (2004) in *Arabidopsis thaliana* seeds and by Zhu *et al*. (2009) in rice. Deckers *et al*. (2004) postulated that this inhibition is independent of the function of hexokinase (HXK).

These authors suggest that there is an independent regulatory pathway of ABI2/ABI4/ABI5, that is, there is more than one signaling pathway involved in the delay of glucose-induced germination, which suggests that the IP3K-Akt signaling pathway could be involved in the delay observed by the combination of glucose and glucokinin, which explains their additive effect. In the inner region of the *C. ensiformis* testa, Oliveira *et al*. (2004) located a Gao, Gao receptor proteins, and a phosphoserine-like protein, so they related Gao with the signaling pathway of carbohydrate transport into the embryo.

Apparently, an increase in the concentration of free sugars within the seed does not favor germination, contrary to the idea that it provides a quickly accessible source of energy. Zhu *et al*. (2009) hypothesized that the delay in germination is the result of high concentrations of free sugars, which promote the suppression of ABA catabolism due to an inhibition in the transcription of ABA 8-hydroxylases that participate in the conversion of ABA to phaseic acid. This could be related to the additive effect of the combined treatment at 9 DASI.

In the case of the emergence, none of the treatments showed significant differences in the speed of emergence, among them or compared to the control, during the time analyzed (Table 2). The speed values were 5.4 ±0.15 plants day^{-1} for the control, 4.6 ±0.54 for Gao, 5.3 ±0.71 for glucose and 5.3 ±0.4 for the combination. It is interesting that, despite the difference in oCG$_{max}$ at 9 DASI, due to the rate of inhibition during germination, after transplantation, the behavior of CE, ET50, and the emergence speed of all effectors was uniform compared to the control from 9 to 19 DASI (Figure 2B).

Table 2. Physiological parameters in the emergence of samples of *C. chinense* (Jacq.) treated with the control, Gao, glucose, and the combination.

Treatment	Emergence (9 -15 DASI)			
	CE$_{max}$ (%)†	ET$_{50}$ ††	Spe†††	RtInd
Control	90 ±8.2^{A}	13.5 ±0.4^{A}	5.4 ±0.15 ^{A}	0
Gao	87 ±0.9^{A}	13 ±1^{A}	4.6 ±0.54 ^{A}	0
Glucose	93 ±5^{A}	12.7 ±0.3^{A}	5.3 ±0.71 ^{A}	0
Gao/Glu	91.6 ±6^{A}	13.2 ±1^{A}	5.3±0.4 ^{A}	0

† = maximum observed percentage of seedlings emerged; ††= day after the start of imbibition (DASI) where 50% of the population has met the exclusion criteria; †††= speed, expressed as number individuals/day. Different letters indicate significant differences between treatments (Tukey ≤ 0.05).

The oCE$_{max}$ also showed no significant differences between treatments, although it reached 91 ±2.5% in the samples treated with glucose and 93 ±5% with the Gao+glucose combination. For their part, the control and the Gao treatment also showed similar values for the percentage of oCE$_{max}$, 87.2 ±2.5 and 85 ±5.8%, respectively. This suggests that the seeds did not present irreversible damage or stress as a result of the treatments during their germination stage, nor during transplantation and/or emergence.

The differential behavior of the response to the treatment of Gao and Gao+glucose in germination and emergence may be due to the fact that the hormonal overregulation of ABA disappears when the seeds are transplanted, which triggers the already widely reported compensatory effects to take place in the embryo, including: increased cell proliferation in the meristems (Garrocho-Villegas *et al*., 2013) and increase in de novo synthesis of proteins and ribosomes (Avila-Alejandre *et al*., 2013; Villa-Hernández *et al*., 2013).

During establishment (Figure 2C), it was observed that all treatments (Gao, glucose, or the combination) significantly increased the total percentage of established seedlings ($p \leq 0.05$) compared to the control from day 19, and this effect was maintained until 22 DASI.

The induction speed of the establishment of the different treatments in comparison to the control was as follows: 60.78% for Gao, 50.98% for glucose, and 45.1% for the Gao+glucose combination (Table 3). All treatments significantly increased the oCEst$_{max}$ compared to the control at 22 DASI (Figure 2C). For the control, it was 51 ±10%, whereas for Gao, it was 82.1 ±11% and for glucose and the combination, 77 ±14% and 74 ±9%, respectively.

Table 3. Physiological parameters in the establishment of samples of *C. chinense* (Jacq.) treated with the control, Gao, glucose and the combination.

Treatment	Establishment (15-22 DASI)			
	CEst$_{max}$ (%)†	EstT$_{50}$ ††	Spe†††	RtInd (%)
Control	51 ±10^{B}	21 ±2.7 ^{B}	0.68 ±0.3 ^{B}	0
Gao	82 ±11^{A}	17.6 ±0.7 ^{A}	2.7 ±0.76 ^{A}	60.78
Glucose	77 ±14^{A}	18.06 ±1 ^{A}	1.6 ±0.43 ^{A}	50.98
Gao/Glu	74 ±9^{A}	18.3 ±0.2 ^{A}	1.6 ±0.44 ^{A}	45.1

† = maximum observed percentage of seedlings established on the final day of each stage; ††= day after the start of imbibition (DASI) where 50% of the population has met the exclusion criteria; †††= speed, expressed as number individuals/day. Different letters indicate significant differences between treatments (Tukey# 0.05).

As for the EstT50, it was significantly lower (*p*# 0.05) in all treatments; in the control, it was 21.8 ±2.7 DASI, whereas for Gao, it was 17.6 ±0.7 DASI, and for glucose and the combination, it was 18.06 ±1 and 18.3 ±0.2 DASI, respectively. All treatments increased the speed of establishment compared to the control (Table 3), in particular, Gao reached 2.77 ±0.76 plants day^{-1}, whereas the glucose and combination showed very similar values.

Finally, the effect of the treatments on the seedling phenotype was evaluated (Table 4). Gao significantly increased (*p*# 0.05) the length of the taproot and the number of lateral roots compared to the control and the other treatments. All treatments increased the length of the hypocotyl in comparison to the control, but there was no difference between them.

Table 4. Effect of Gao on the phenotype development of *C. chinense* (Jacq.) seedlings at 22 DASI.

Treatment	Num. of lateral roots†	Root length (mm)†	Hypocotyl length (mm)†
Control	2.17 ±0.78^{C}	37.2 ± .8^{B}	8.74 ±1.5^{B}
Gao	4.11 ±1.11^{A}	51 ±8.1^{A}	10.9 ±1.17^{A}
Glucose	2.89 ±1.74^{AB}	40.6 ±11.8^{B}	11 ±1.31^{A}
Gao+Glucose	3.22 ± .78^{BC}	41.7 ±13.9^{AB}	10.2 ±1.35^{A}

† = the data shown corresponds to the final day of the evaluation. The mean and SD of 6 independent experiments are shown, n= 360 seedlings treatment^{-1}. Different letters indicate significant differences between treatments (Tukey≤ 0.05).

The results suggest that the application of all the inducers favored the development of *C. chinense* seedlings (Figure 2); however, they did so in a differential way since, while Gao particularly favored the growth of the root system, glucose treatments or the combination favor the growth of the hypocotyl in comparison to the control (Table 4).

The particular effect of Gao on the root system of *C. chinense* (Jacq.) was similar to that previously reported in corn (Avila-Alejandre *et al*., 2013) and *Arabidopsis thaliana*, where the authors reported an increase in the number of root hairs, lateral roots, and vegetative development (Pascual-Morales *et al*., 2012). Although our results cannot be conclusive, it is hypothesized that this effect observed on the radicle growth of *C. chinense* (Jacq.) is induced by signal transduction and gene expression mechanisms (Pascual-Morales *et al*., 2012).

On the other hand, the effect on germination delay and hypocotyl length could be modulated by free reducing sugars, as occurs during the early stages after the mobilization of scutellum reserves, and the delay observed by the authors after the administration of exogenous glucose. Related to the above, it has been proposed that compounds such as glucose fulfill other functions in addition to providing energy to metabolism, depending on the tissue and stage of development; for example, it has been proposed that glucose and other simple sugars can function as osmotic regulators and participate in the protrusion of the radicle (Wang *et al*., 2021).

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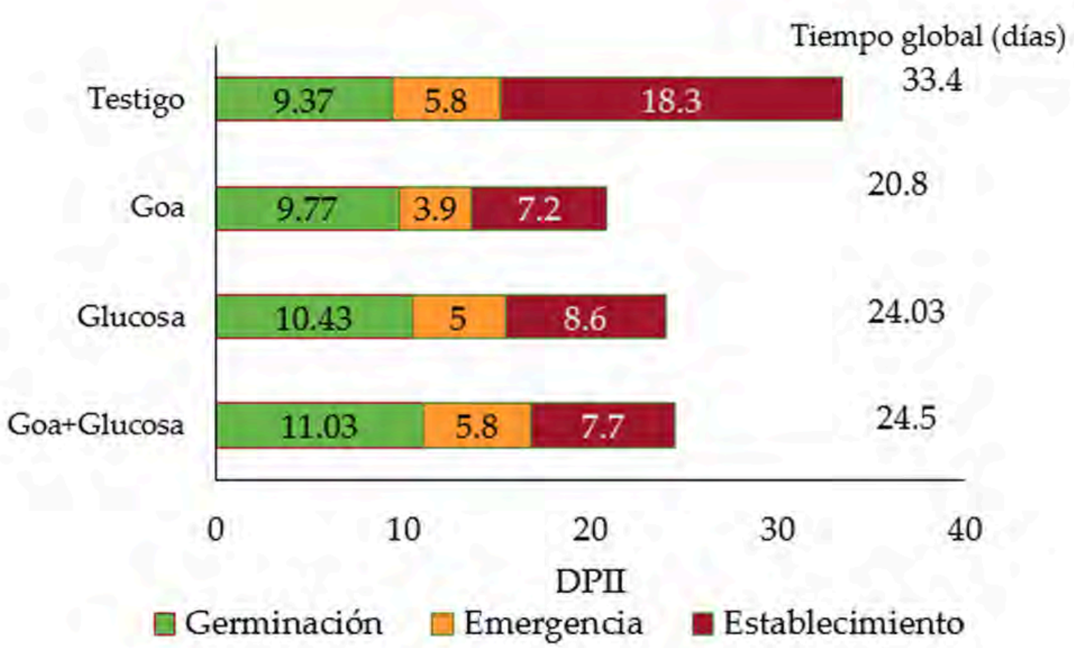
Additionally, in *Arabidopsis*, it has been reported that the meristematic zone of the root responds in a dose-dependent manner to the concentration of glucose, at low concentrations, the length of the root increases, whereas at high concentrations, it decreases (Siddiqui *et al*., 2020), in addition to the fact that sugars and cytokinins act synergistically to regulate the emergence of seedlings, the activation of meristems, branching, and flowering of *Arabidopsis* shoots (Wang *et al*., 2021).

Finally, the overall treatment times during the early development of *C. chinense* (Jacq.) were compared (Figure 3), which were defined as the estimated time at which 90% of seedlings reach the inclusion criterion in the corresponding stage, which was inferred using the PROBIT method. All treatments increased the time needed to reach 90% germination.

Figure 3. Effect of inducers on the global time of establishment of *C. chinense* (Jacq.). The iGT90, iET90 and iEstT90 are plotted. All three inducers decrease overall time by decreasing emergence time and establishment.



The most important effect of the inducers was on iEstT90; all treatments significantly reduced the overall time at which 90% of the establishment was reached. The shortest overall time occurred with the treatment of Gao, 20.8 DASI, followed by glucose with 24.03 DASI, and at the end, the combined treatment, 24.5 DASI (Figure 3). That is, compared to the control, the time the seedlings stay in the germination chambers is reduced by up to 10 days (equivalent to a 30% reduction) with the treatment of Gao, by nine days (equivalent to a 26% reduction) with glucose and by 8.8 days (equivalent to a 26.3% reduction) with the combination; nevertheless, there are no differences (*p*# 0.05) between both treatments.

The reduction of the establishment time and the effect on the development of the root system obtained by the application of Gao are results that show its probable use as a biostimulant and it could be highly appreciated in PA (Magdaleno-Hernández *et al*., 2016) as an alternative that optimizes the space within the production modules and could reduce the stay time of seedlings without the need for genetic improvement (Hernández-López *et al*., 2018) or chemical fertilization and could speed up production by reducing costs.

Although the mechanisms of action of Gao or glucose at the molecular level were not evaluated in this work, it is proposed in a future work to explore this approach to corroborate the role of some

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important regulators such as hexokinase (HXK) and TOR protein, two main sensors of nutrient and energy status (Sánchez-Linares *et al*., 2012, Garrocho-Villegas *et al*., 2013; Díaz-Granados *et al*., 2020; Meng *et al*., 2022).

Conclusions

The results indicate that exogenous glucose administration delays germination, but neither glucose nor its combination affects the phenotype of seedlings in the emergence phase. Despite the delay in germination, treatments outperformed the control, suggesting the occurrence of physiological and molecular events known in other models. In habanero chilis, the application of Gao uniformizes emergence and reduces seedling establishment time compared to the control.

Treatment with Gao increased root growth, whereas glucose increased hypocotyl growth; it is proposed that the application of Gao or glucose may be useful to optimize the cultivation time of habanero chilis in protected agriculture (PA); nonetheless, the effect is different. Although this study did not include molecular evidence, it is not ruled out that the mechanism is the one already reported by other authors for these processes, which could be investigated in future studies.

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