



Plant growth regulators influence the height and biomass partition of castor plants¹

Reguladores de crescimento influenciam a altura e a partição de biomassa de plantas de mamona

Liv S. Severino^{2*} & Eduarda de Oliveira³

¹ Research developed at Embrapa Agrossilvipastoril, Sinop, MT, Brazil

² Embrapa Algodão, Sinop, MT, Brazil

³ Instituto Federal de Mato Grosso, Campo Novo do Parecis, MT, Brazil

HIGHLIGHTS:

Trinexapac-ethyl restricts height growth of castor plants, but it impairs root growth.

Chlormequat and mepiquat chloride are effective for restricting castor plant height growth only in very high dose.

Disturbance on biomass allocation among root, stem, and leaves is a side effect of plant growth regulators.

ABSTRACT: Castor (*Ricinus communis*) is a drought-resistant oilseed crop. This study evaluated five plant growth regulators (PGR) on their capacity to influence stem elongation of castor plants growing under shade and measured side effects on the biomass allocation among leaf, stem, and roots. The experiment had 220 castor plants of the cultivar AKB 02, on a completely randomized design and four replicates. The plants were kept under artificial shade and treated with 11 doses of PGR, applied in the first day after emergence. Eight plants were exposed to full sun radiation without PGR treatment. The plant height was measured daily, and the plants were harvested for weighing the final biomass. The data was subjected to multiple linear regression. The shade promoted stem elongation and reduced biomass accumulation in all compartments. The height growth was restricted by trinexapac-ethyl, mepiquat chloride, and chlormequat chloride. Gibberellin promoted stem elongation in addition to the shade effect. Paclobutrazol did not influence stem elongation, but it favored biomass accumulation and increased the stem density. Gibberellin promoted allocation to stem replacing leaf biomass; trinexapac-ethyl promoted root replacing stem and leaf biomass; mepiquat and chlormequat chloride promoted stem in detriment of leaf biomass. In conclusion, plant growth regulators may be effective to restrict height growth of castor plants, but they can also disturb the biomass allocation among root, stem, and leaves.

Key words: *Ricinus communis*, chlormequat chloride, gibberellin, mepiquat chloride, paclobutrazol, trinexapac-ethyl

RESUMO: Mamona (*Ricinus communis*) é uma planta oleaginosa resistente à seca. Este estudo avaliou cinco reguladores de crescimento quanto a sua capacidade de influenciar o alongamento do caule de plantas de mamona submetidas a sombreamento e mediu efeitos colaterais sobre a alocação de biomassa entre raízes, caule e folhas. O experimento utilizou 220 plantas de mamona da cultivar AKB 02 em delineamento inteiramente casualizado com quatro repetições. As plantas foram submetidas a sombra artificial e tratadas com 11 doses de reguladores de crescimento aplicados no primeiro dia após a emergência. Oito plantas foram expostas ao sol, sem tratamento com reguladores de crescimento. A altura das plantas foi medida diariamente e as plantas foram colhidas para pesar a biomassa final. Os dados foram analisados por regressão linear múltipla. O sombreamento causou alongamento do caule e reduziu o acúmulo de biomassa em todos os compartimentos. O crescimento em altura foi restringido pelo trinexapac-etil, cloreto de mepiquat e cloreto de chlormequat. A giberelina promoveu alongamento do caule adicional ao efeito do sombreamento. O trinexapac-etil favoreceu as raízes em detrimento de caule e folhas. Cloreto de chlormequat e de mepiquat favoreceram a alocação de biomassa para o caule em detrimento de folhas. Em conclusão, reguladores de crescimento podem ser efetivos para restringir o crescimento em altura de plantas de mamona, mas eles também podem alterar a alocação de biomassa entre raízes, caule e folhas.

Palavras-chave: *Ricinus communis*, giberelina, cloreto de chlormequat, cloreto de mepiquat, paclobutrazol, trinexapac-etil



INTRODUCTION

Castor (*Ricinus communis*), Euphorbiaceae, is predominantly cultivated in semi-arid regions of the world for producing castor oil, which is a valued raw material in the chemical industry. The high plasticity of castor plant favors excessive height growth when the growing conditions are out of the optimal range, such as excessive irrigation, high plant density, unbalanced soil fertility, or intense cloudiness. Studies on plant growth regulators (PGR) on castor crop are very scarce despite their importance to restrict height growth, to prevent lodging, to improve the efficiency of mechanized harvest, and to prevent microclimate favorable to diseases. Most of the previous attempts to restrict castor plant height with PGR were unsuccessful. Mepiquat chloride either did not influence height growth, or it had the opposite effect (Campbell et al., 2014; Oswalt et al., 2014). Presently, there is no report of recommended PGR for castor crop.

Trinexapac-ethyl, paclobutrazol, mepiquat chloride, and chlormequat chloride are PGR that inhibit the synthesis of gibberellins and are used aiming to restrict the height growth of plants and several other characteristics, such as the leaf color for ornamental purpose (Teixeira et al., 2022), the rate of lodging (Souza et al., 2022), tillering (Ervin & Koski, 1998), time for flowering (Kupke et al., 2022), time for seed maturation (Qi et al., 2022), and seed yield (Ferrari et al., 2022). Gibberellin, with the opposite effect, is the main hormone for the promotion of stem elongation, and it is also used for promoting seed germination and flowering of many species (Castro-Camba et al., 2022), to improve yield and quality of mung bean (*Vigna radiata*) (Islam et al., 2021), and to promote rooting and initial growth of *Spondias tuberosa* seedlings (Matos et al., 2020).

This study evaluated five plant growth regulators on their capacity to influence stem elongation of castor plants growing under artificial shade and measured side effects on the biomass allocation among leaf, stem, and root.

MATERIAL AND METHODS

This experiment was conducted in a greenhouse with roof and lateral walls made of polycarbonate, located in Sinop (11.9 S, 55.6 W, 390 m a.s.l.), State of Mato Grosso, Brazil, in October 2021. Castor seeds of the cultivar AKB 02, provided by Terasol, were pre-germinated in moisturized paper, at constant temperature of 30 °C for 48 hours, in the dark. The number of seeds subjected to pre-germination was twice the number to be used in the experiment aiming to select only the seeds with

radicle protrusion aiming to reduce the variability caused by uneven germination. Germinated seeds were planted 2 cm deep, in 220 square plastic containers (5.2 x 5.2 x 7.4 cm), filled with a mix of soil and organic substrate (1:1 v:v), and held in 20-cells trays. Eight plants were exposed to full sun radiation, and they were not treated with PGR. All the other plants were subjected to artificial shade aiming to simulate the most common condition that induces height growth, particularly when the field has excessive plant density and there is intense competition for light. In order to create a shaded environment, a 50% shade screen was placed 25 cm above the plants. The plants were watered daily (5 mm day⁻¹) with an automated sprinkler irrigation system, except in the 24 hours after PGR treatment to prevent washing the substances applied on the leaf. During the experiment, the air temperature under the shade and close to the leaves varied from 23.2 ± 1.0 to 37.3 ± 2.5 °C, and the substrate's temperature varied from 23.5 ± 1.0 to 34.5 ± 2.3 °C.

The expression "plant growth regulator" (PGR) was used indistinctly for substances that promote height growth (gibberellin) or retard height growth (trinexapac-ethyl, paclobutrazol, mepiquat chloride, and chlormequat chloride). The treatments consisted of a control treatment (without any PGR) and ten doses of each PGR (Table 1). The commercial products used were ProGibb 400[®] (gibberellin), Moddus[®] (trinexapac-ethyl), paclobutrazol P.A., Pix HC[®] (mepiquat chloride), and Tuval[®] (chlormequat chloride).

The PGR solutions were applied on the first day after emergence, when the stem was upright, only to the plants under shade. Despite the pre-germination procedure, the emergence occurred for 5 days. The option was made to apply the treatments to the plants exactly in the first day after emergence on different days instead of applying them in the same day but in plants with varying age. For that reason, the treatments were not applied in the same day to all plants, but according to the number of emerged plants in each day: gibberellin (day 1), trinexapac-ethyl (days 1 and 2), paclobutrazol (day 3), mepiquat chloride and chlormequat chloride (days 1, 2, and 3). Plants were assigned to the dose zero (control) under shade on day 1 and to the control at full sun radiation on days 2 and 3. The date of treatment application and harvest was registered for each individual plant.

The solutions were prepared on the first day and kept under refrigeration at 4 °C for the following days. The PGR was applied dripping 50 µL of the solution in each cotyledonary leaf and spreading the drop with a soft brush through the leaf blade, apical bud, and petiole. Each combination of PGR and dose was applied once on four plants (replicates) in a completely randomized

Table 1. Doses (mg L⁻¹ a.i.) of plant growth regulators applied on castor plants

Dose	Gibberellin	Trinexapac-ethyl	Paclobutrazol (mg L ⁻¹ a.i.)	Mepiquat chloride	Chlormequat chloride
1	8	10	20	500	160
2	14	17	34	1000	320
3	22	28	56	1500	480
4	37	46	92	2000	640
5	62	77	154	2500	800
6	103	129	258	3000	960
7	172	215	430	3500	1120
8	287	359	718	4000	1280
9	479	599	1198	4500	1440
10	800	1000	2000	5000	1600

design. Immediately after treatment, the plants were placed in the trays in positions that were randomly assigned mixing all the treatments (except the plants exposed to full sun radiation). Four plants were not treated with any solution to act as a control under shade condition. Another eight plants were assigned to a control under full sun radiation (inside the greenhouse), and they were kept at least 20 cm distant each other to prevent cross-shading.

Plant height was registered daily, measuring the distance between the substrate surface and the point of insertion of the cotyledonary leaves in the stem. The plants were harvested at different times after emergence aiming to measure the progress of biomass accumulation. For that purpose, the plants were harvested either after reaching the height of 22 cm (as the leaves approached the shading screen), or some plants were randomly selected to be harvested between 4 and 10 days after emergence. At harvest, each plant had the roots carefully washed and was separated into root, stem, and leaves, oven-dried for 48 hours at 65 °C, and weighed.

The dry weights of roots, stem, and leaves were used to calculate total biomass (sum of the three components), biomass allocation to roots, stem, and leaves (weight of each component / total biomass), and stem density (stem weight / plant height in the day of harvest). The data of plants exposed to full sun radiation and plants under shade without PGR treatment (control under shade) were analyzed using simple linear regression with the model

$$Y = \alpha + \beta_1 X_1 + \varepsilon$$

where:

α , and β_1 - regression coefficients; and
 X_1 - number of days after emergence.

The data on plants treated with PGR were analyzed using multiple linear regression with the model

$$Y = \alpha + \beta_1 X_1 + \beta_2 X_2 + \varepsilon$$

where:

α , β_1 , and β_2 - regression coefficients;
 X_1 - number of days after emergence; and
 X_2 - dose of the plant growth regulator.

For standardization, the X_2 values were expressed as the percentage of the maximum dose (varying from 0 to 100). A multiple linear regression equation was calculated for each PGR and for each growth variable. The data from the plants under shade without PGR treatment was used in both the simple linear regression analysis in function of days after emergence (X_1) and in the multiple regression analyses as the control ($X_2 = 0$). The significance of each regression coefficient was calculated with t test, dividing the regression coefficient by its standard error ($t = \beta_n / se_n$). The significance was calculated considering the degrees of freedom of the error from the regression analysis. The coefficient was considered significant when $p \leq 0.1$.

The regression equations and the coefficient of determination (R^2) were presented in tables and used to calculate the regression lines presented in figures. The regression coefficient was

omitted from the equation when it was not significant. When both coefficients were not significant, only the average was presented, and the R^2 was omitted. The individual data points were not displayed because the graphs would be too polluted. The progress of growth (in function of time) was presented in figures fixing the value of the dose to the maximum ($X_2 = 100$) and assigning values for X_1 varying from the minimum to the maximum number of days after emergence in which plants were harvested for that specific treatment. The effect of the PGR doses was presented in figures fixing the number of days after emergence ($X_1 = 6$ for paclobutrazol and $X_1 = 8$ for all the other PGR) and assigning values for X_2 varying from 0 to 100. The regression line was omitted from figures when the coefficient was not significant. The regression coefficient of the plant height in function of the days after emergence was assumed as an estimation of the height growth rate.

RESULTS AND DISCUSSION

When castor plants were exposed to full sun light, the height growth rate was of 0.35 cm day⁻¹ ($p \leq 0.01$, Table 2). The total biomass increased at the rate of 68.93 mg day⁻¹ ($p = 0.07$, Figure 1E), and it was allocated predominantly to the leaves, which grew at the rate of 61.44 mg day⁻¹ ($p = 0.01$, Figure 1D), while the growth was not significant in root ($p = 0.86$) and stem biomass ($p = 0.41$). As the assimilated carbon in the plants exposed to full sun radiation was preferentially allocated to the leaves, the partition to root and stem reduced along the time (Figures 1F and G). The stem density of castor plants exposed to full sun light increased at the rate of 1.38 mg cm⁻¹ day⁻¹ (Figure 1I). When growing exposed to full sun radiation, which is the regular condition for agricultural production, the carbon assimilated by photosynthesis in the first days after emergence was preferentially allocated to grow leaves (considering that water and nutrients were abundant). Castor plants evolved to grow exposed to full sun radiation, and light-demanding species usually allocate most of the assimilated carbon to above-ground structures (Giertych et al., 2015). As sun radiation was plenty available and there was not competition among plants for light, stem elongation was minimal, and the biomass allocated to that compartment promoted increased stem density.

Under shade and without treatment with any PGR, the stem of castor plants elongated at the rate of 0.76 cm day⁻¹ (Table 2), which was more than twice the rate observed on castor plants growing exposed to full sun radiation, demonstrating the plasticity for height growth at early stages of development. Because of the reduced photosynthesis under shade, the accumulation of biomass was not significant in any compartment. Compared to the plants growing at full sun radiation, the shaded plants reduced the rate of biomass accumulation from 68.93 to 21.95 mg day⁻¹, and the plants adjusted the biomass allocation, favoring the stem instead of the leaves.

Gibberellin promoted height growth (Figure 1A), and the effect was proportional to the dose of the hormone (Figure 2A). The rate of height growth (1.80 cm day⁻¹) was approximately twice that of the shaded plants without PGR treatment (Table

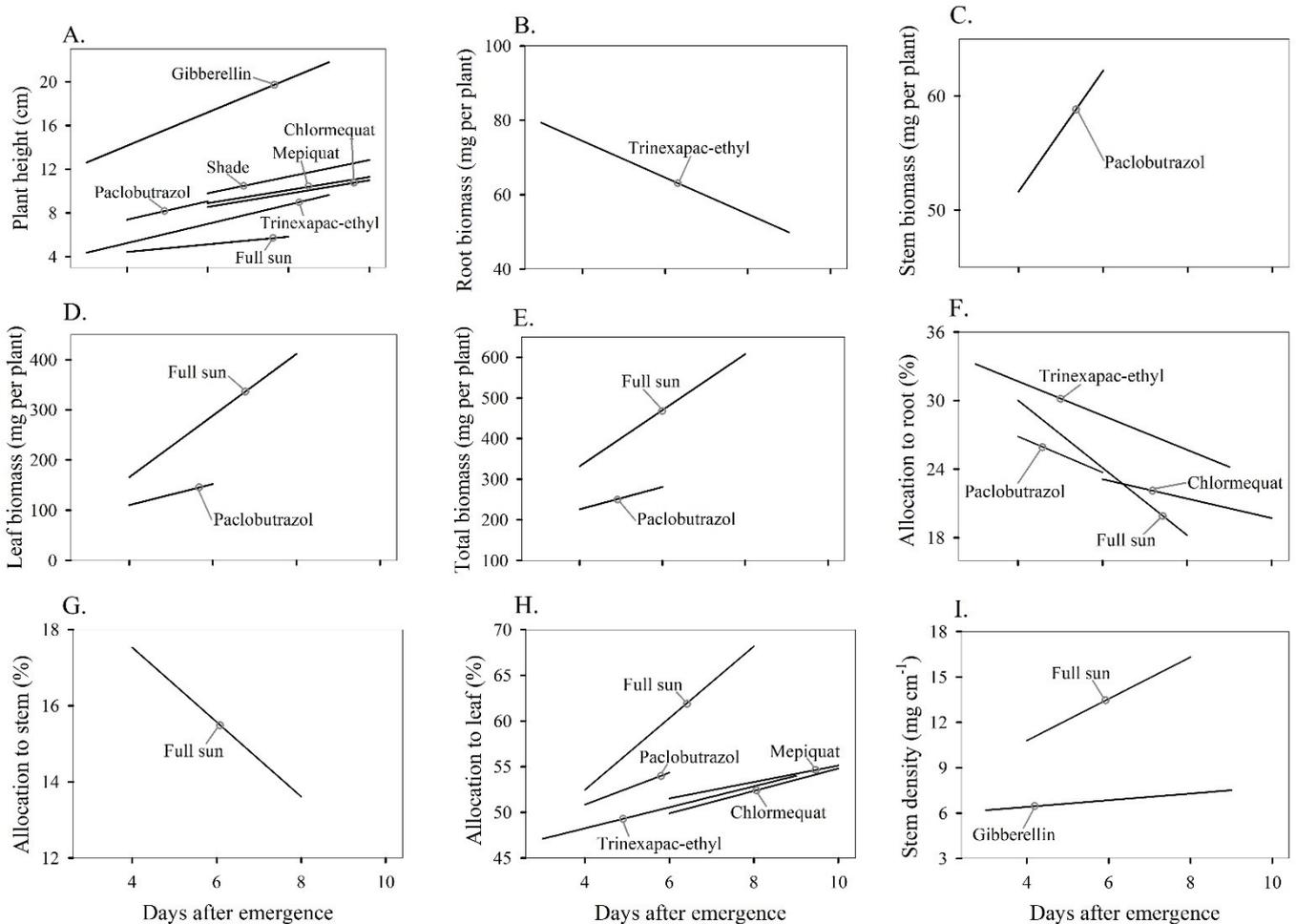


Figure 1. Evolution of plant height (A), biomass of root (B), stem (C), leaf (D), and total biomass (E), allocation of biomass to root (F), stem (G), and leaf (H), and stem density (I) of castor plants under full sun radiation or under shade and treated with plant growth regulators

2). Nevertheless, gibberellin promoted only stem elongation, while the plant's total biomass was unaffected. Only the stem biomass increased proportionally to the doses of gibberellin (Figure 2C), and the preferential compartment for biomass allocation shifted from the leaf to the stem. The biomass allocated to the stem was spent on elongation in a way that the stem density did not change in response to the doses of the hormone. Gibberellin plays a pivotal role in the coordination of growth and development of plants, particularly on the regulation of cell elongation. The shaded environment would naturally favor height growth in castor plants as an attempt to outgrow neighboring competitor plants. It was observed in this study that the exogenous hormone promoted additional height growth (Figure 3A). There are reports of gibberellin influencing the height growth of castor plants, but in general this hormone does not influence the total biomass accumulation or its allocation among compartments as observed under stressing conditions such as high content of Cadmium in the soil (Hadi et al., 2021) or under salt stress (Zhou et al., 2014; Jiao et al., 2019). It is unlikely that gibberellin would be sprayed in castor crop for promoting height growth, but it is important to register this side effect in case the hormone is used for other purposes such as improving germination (Severino, 2023a), delaying flower initiation, or promoting the production of female flowers (Shifriss, 1961).

Trinexapac-ethyl was effective for restricting the height growth of castor plants; however, it also affected the total biomass accumulation. The root biomass reduced over time (Figure 1B), while the increasing doses were associated with less biomass allocated to stem and leaf (Figure 2D) and with reduced total biomass (Figure 2E). The most detrimental effect of trinexapac-ethyl was observed on the biomass allocated to the root, which reduced along the time (Figure 1F) but increased in response to the dose of this PGR (Figure 2F). The effect of trinexapac-ethyl on the restriction of castor plant height growth was the most intense among the PGR evaluated (Figure 3B); however, this substance reduced the overall plant growth as side effect. It was also observed that trinexapac-ethyl influenced root morphology, causing some roots to become thicker and inhibiting the growth of fine roots. Root diameter was not measured as an experimental variable, but it was just noticed when the roots were washed from the substrate.

Paclobutrazol applied on the leaf was not effective as height growth retardant in castor plants (Table 3); however, it favored biomass accumulation in stem (Figure 1C), leaf (Figure 1D), and total biomass (Figure 1E), despite the shade restriction. For comparison, all the other PGR were detrimental or ineffective for biomass accumulation in stems and leaves. Paclobutrazol also favored the partition of biomass to leaves (Figure 1H), and it increased stem density proportionally to the dose (Figure 2I).

Table 2. Linear and multiple regression equations⁽¹⁾ of growth and biomass allocation of castor plants (Y) in function of days after emergence (X_1) and doses of gibberellin and trinexapac-ethyl⁽²⁾ (X_2 , 0-100%)

Growth variable	Regression equation	R ²	CV (%)
Control - full sun radiation			
Plant height (cm)	$Y=3.02+0.35*X_1$	0.30	29.6
Root biomass (g)	$Y=98.18$		37.1
Stem biomass (g)	$Y=38.15$		36.5
Leaf biomass (g)	$Y=-80.03+61.44*X_1$	0.69	23.5
Total biomass (g)	$Y=56.30+68.93*X_1$	0.46	26.3
Allocation to root (%)	$Y=41.82-2.95*X_1$	0.62	16.4
Allocation to stem (%)	$Y=21.45-0.98*X_1$	0.46	11.6
Allocation to leaf (%)	$Y=36.73+3.93*X_1$	0.66	7.82
Stem density (mg cm ⁻¹)	$Y=5.27+1.38*X_1$	0.48	17.5
Control - under shade			
Plant height (cm)	$Y=5.26+0.76*X_1$	0.58	22.0
Root biomass (g)	$Y=50.03$		21.5
Stem biomass (g)	$Y=29.57$		24.0
Leaf biomass (g)	$Y=93.52$		17.7
Total biomass (g)	$Y=173.12$		18.5
Allocation to root (%)	$Y=24.83$		13.1
Allocation to stem (%)	$Y=19.16$		9.1
Allocation to leaf (%)	$Y=56.01$		3.5
Stem density (mg cm ⁻¹)	$Y=2.59$		18.2
Gibberellin			
Plant height (cm)	$Y=2.71+1.80*X_1+0.05*X_2$	0.72	61.3
Root biomass (g)	$Y=55.98$		27.3
Stem biomass (g)	$Y=100.74+0.24*X_2$	0.21	22.6
Leaf biomass (g)	$Y=130.29$		23.5
Total biomass (g)	$Y=287.01$		21.0
Allocation to root (%)	$Y=19.09$		15.1
Allocation to stem (%)	$Y=33.26$		14.9
Allocation to leaf (%)	$Y=47.65$		7.1
Stem density (mg cm ⁻¹)	$Y=4.53+0.22*X_1$	0.07	15.2
Trinexapac-ethyl			
Plant height (cm)	$Y=4.66+0.86*X_1-0.03*X_2$	0.65	47.3
Root biomass (g)	$Y=88.73-3.28*X_1$	0.08	22.0
Stem biomass (g)	$Y=76.43-0.32*X_2$	0.23	24.6
Leaf biomass (g)	$Y=157.41-0.69*X_2$	0.28	21.0
Total biomass (g)	$Y=322.58-1.05*X_2$	0.21	19.8
Allocation to root (%)	$Y=27.40-1.01*X_1+0.08*X_2$	0.48	15.4
Allocation to stem (%)	$Y=23.64+0.03*X_2$	0.23	11.3
Allocation to leaf (%)	$Y=48.96+0.98*X_1-0.05*X_2$	0.41	4.8
Stem density (mg cm ⁻¹)	$Y=7.83+0.01*X_2$	0.12	18.2

⁽¹⁾ The regression coefficient was omitted when it was not significant ($p \leq 0.10$). ⁽²⁾ The maximum doses were 0.8 g L⁻¹ a.i. of gibberellin and 1 g L⁻¹ a.i. of trinexapac-ethyl

There was no previous report of paclobutrazol applied on castor plants for retarding height growth. The only previous study was made by Witchard (1997), who measured the translocation of paclobutrazol in castor plants without searching for growth regulation, but just using castor as a model plant to demonstrate that this substance is somewhat mobile in the phloem and not only in the xylem. Anyway, paclobutrazol deserves further evaluation on castor plants because of the significant biomass accumulation and increased stem density despite the shade effect. This short-term study at greenhouse conditions cannot be extrapolated to field conditions, but that observation just calls attention to the possibility of agronomical use of this PGR, as suggested for sesame (Mehmood et al., 2021), ornamental cauliflower (Teixeira et al., 2022), and turmeric (Chungloo et al., 2021).

Mepiquat chloride restricted the height growth of castor plants (Table 3); however, the restricted height growth came

at the cost of reduced accumulation of leaf and total biomass (Figures 2D and E). As the dose of this PGR increased, a trade-off occurred between the increased biomass allocated to the stem (Figure 2G) and the reduced biomass allocated to the leaves (Figure 2H), while the stem density was not influenced. Mepiquat chloride was reported in several studies with little or no effect for restricting castor plant height (Campbell et al., 2014; Oswald et al., 2014), and only in the report made by Souza-Schlick et al. (2018) this PGR reduced height growth at both greenhouse and field conditions, and it also caused similar reduction of leaf biomass, while stem biomass was not influenced. It should be considered that the highest dose of mepiquat chloride tested in the present study was 10 times higher than would be regularly sprayed, for example, on a cotton field to manage height growth (Balkcom et al., 2022; Chalise et al., 2022). A preliminary study was made applying doses in the common range of agronomical recommendation, but no effect was observed (the results of that preliminary experiment were not reported). Mepiquat chloride could be further evaluated for managing castor crop because it is a common product that is often used in cotton; however, it should be considered that the requirement for too high doses may turn this PGR cost prohibitive.

Chlormequat chloride was effective for restricting the height growth of shaded castor plants (Figure 2A), but it also reduced the accumulation of root, stem, and leaf biomass (Figures 2B, C, and D). Chlormequat chloride did not influence the stem density neither along time nor in function of the doses (Table 3). Chlormequat chloride also required doses 10 times higher than regular agronomical recommendation to be effective.

Plant growth regulators are employed in agriculture for specific purposes, but they occasionally cause side effects that need to be properly identified and measured. PGR act influencing the synthesis, transport, or degradation of hormones, and for that reason, they may disturb other physiological processes that are controlled by those hormones. Examples of side effect are the reduced height growth of barley (*Hordeum vulgare*) sprayed with trinexapac-ethyl for delaying flowering time (Kupke et al., 2022), the reduction of specific leaf weight of *Spondias tuberosa* seedlings treated with gibberellin for improved rooting (Matos et al., 2020), the reduced sensibility to defoliants and delayed maturity of cotton plants sprayed with mepiquat chloride for chemical pruning (Qi et al., 2022), and the depressed seed yield of soybean treated with paclobutrazol for reducing lodging (Pricinotto & Zucareli, 2014).

This study evaluated the trade-offs in biomass allocation as a side effect of PGR intended only for the specific purpose of restricting castor plant height growth. The plants were subjected to shade because that condition would favor stem elongation, while the PGR would be tested on their capacity to counteract or add to the shade effect. Biomass allocation is a "smart decision" (Severino, 2021) that plants make considering the resources limitation and the demand from each compartment. The plant needs to balance the need for more roots to get water and nutrients, for a long stem to outgrow competitor plants, and for large leaves to harvest light and make

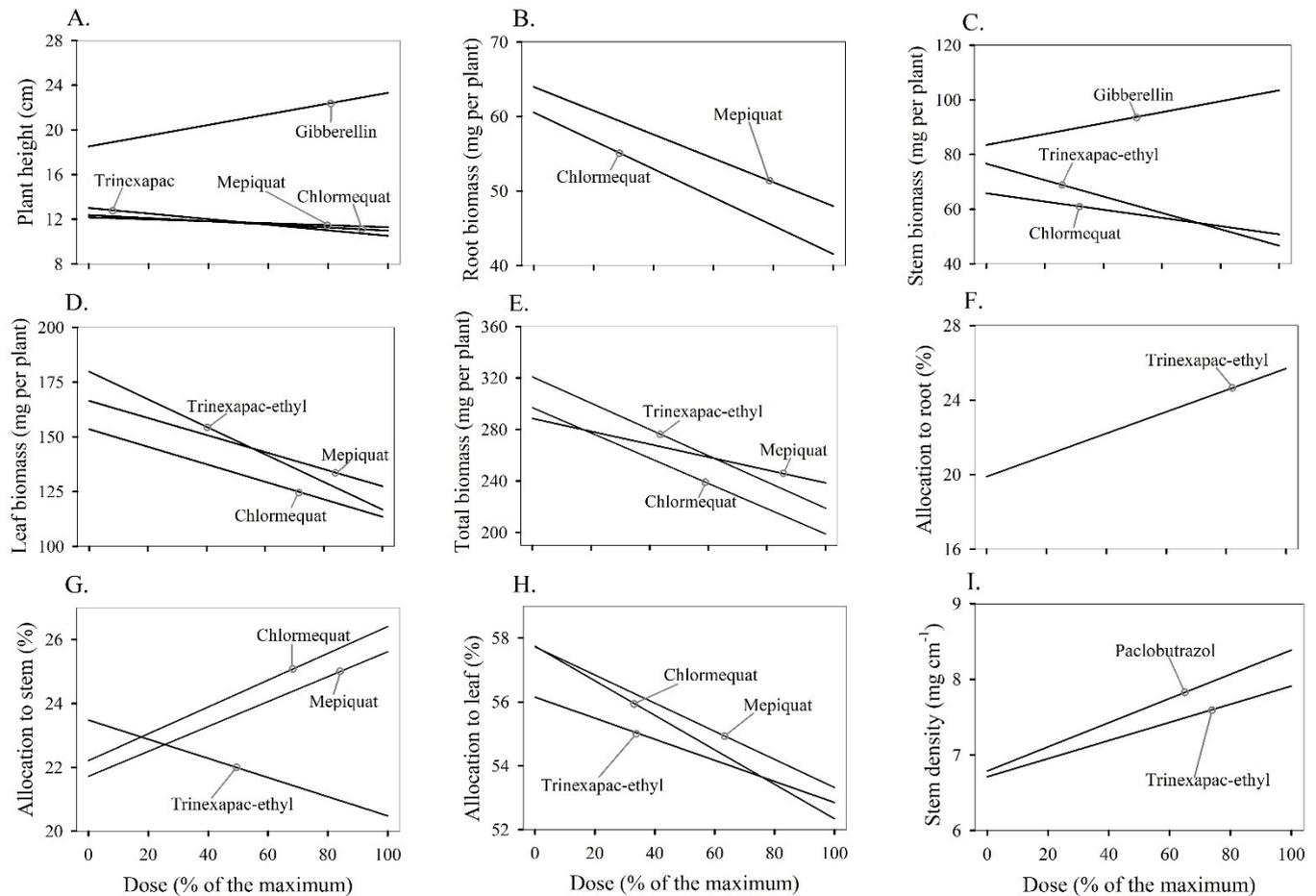


Figure 2. Doses of plant growth regulators influencing the plant height (A), biomass of root (B), stem (C), and leaf (D), total biomass (E), allocation of biomass to root (F), stem (G), and leaf (H), and stem density of castor plants growing under shade



Figure 3. The height growth of castor plants growing under shade was promoted by gibberellin (A) and restricted by trinexapac-ethyl (B) applied on the leaves in the first day after emergence. The doses increase from left (control) to the right (100% of the maximum dose)

photosynthesis. Such decisions are mediated by hormones, and the PGR may deviate the plant from the optimal decisions (Kalbfuß et al., 2022).

Some trade-offs were indeed observed on castor plants. The increasing doses of trinexapac-ethyl caused a trade-off

between the increased biomass allocation to the roots and the reduced allocation to stem and leaf. For comparison, in the absence of trinexapac-ethyl, the biomass was distributed among the three compartments approximately in the same proportion. The trade-off on plants treated with gibberellin occurred between the root (reduced) and the stem (increased). Mepiquat and chlormequat chloride caused trade-off between the stem (increased) and the leaf biomass (reduced).

It should not be assumed that these PGR will always cause the same trade-off in any circumstance. The hypothesis tested was that PGR, as hormonal products, potentially interfere with the biomass allocation as a side effect. Overall, instead of searching for predictable trade-offs for each PGR, it would be better assuming that the biomass allocation follows the Optimal Partitioning Theory (Umaña et al., 2021), in which depending on the environmental conditions and phase of development the plant allocates biomass aiming to maximize its growth taking into consideration which resources are limited or abundant. This study was performed with plants in a very early phase of development, presumably without limitation of water and nutrients, and only light was a limiting resource in the plants subjected to shade. If castor plants were exposed to a different combination of limited or abundant resources, the trade-offs associated with each PGR would be potentially divergent.

The raw data obtained in this study is publically available at Severino (2023b).

Table 3. Multiple regression equations⁽¹⁾ of growth and biomass allocation of castor plants (Y) in function of days after emergence (X_1) and doses of mepiquat chloride, chlormequat chloride, or paclobutrazol⁽²⁾ (X_2 , 0-100%)

Growth variable	Regression equation	R ²	CV (%)
Mepiquat chloride			
Plant height (cm)	$Y=5.84+0.62*X_1-0.01*X_2$	0.45	26.97
Root biomass (g)	$Y=75.17-0.16*X_2$	0.17	23.78
Stem biomass (g)	$Y=69.28$		23.77
Leaf biomass (g)	$Y=158.32-0.60*X_2$	0.21	23.92
Total biomass (g)	$Y=302.77-0.87*X_2$	0.18	21.66
Allocation to root (%)	$Y=24.87$		15.08
Allocation to stem (%)	$Y=24.53+0.04*X_2$	0.15	13.52
Allocation to leaf (%)	$Y=50.60+0.89*X_1-0.04*X_2$	0.14	7.04
Stem density (mg cm ⁻¹)	$Y=5.71$		21.31
Chlormequat chloride			
Plant height (cm)	$Y=5.87+0.64*X_1-0.01*X_2$	0.41	30.61
Root biomass (g)	$Y=85.98-0.19*X_2$	0.18	34.42
Stem biomass (g)	$Y=77.57-0.15*X_2$	0.11	29.21
Leaf biomass (g)	$Y=176.29-0.64*X_2$	0.19	34.63
Total biomass (g)	$Y=339.85-0.98*X_2$	0.18	31.04
Allocation to root (%)	$Y=27.49-0.94*X_1$	0.12	16.44
Allocation to stem (%)	$Y=24.29+0.04*X_2$	0.11	17.29
Allocation to leaf (%)	$Y=48.22+1.20*X_1-0.05*X_2$	0.23	7.59
Stem density (mg cm ⁻¹)	$Y=5.30$		24.34
Paclobutrazol			
Plant height (cm)	$Y=4.04+0.82*X_1$	0.42	65.39
Root biomass (g)	$Y=4.38$		27.51
Stem biomass (g)	$Y=29.62+4.39*X_1$	0.09	26.22
Leaf biomass (g)	$Y=15.60+19.87*X_1$	0.19	30.90
Total biomass (g)	$Y=93.60+25.67*X_1$	0.15	26.18
Allocation to root (%)	$Y=32.00-1.45*X_1$	0.13	16.94
Allocation to stem (%)	$Y=25.12$		12.29
Allocation to leaf (%)	$Y=42.88+1.84*X_1$	0.19	7.24
Stem density (mg cm ⁻¹)	$Y=6.73+0.02*X_2$	0.10	23.85

⁽¹⁾ The regression coefficient was omitted when it was not significant. ⁽²⁾ The maximum doses were: 5 g L⁻¹ a.i. of mepiquat chloride, 1.6 g L⁻¹ a.i. of chlormequat chloride, and 2 g L⁻¹ a.i. of paclobutrazol

* The regression coefficient is significant ($p \leq 0.1$)

CONCLUSIONS

1. Trinexapac-ethyl, mepiquat chloride, and chlormequat chloride were effective to restrict stem elongation of castor plants under shade, but the last two required very high doses to be effective.

2. Gibberellin promoted additional stem elongation on top of the height growth caused by the shaded environment.

3. Paclobutrazol did not influence stem elongation, but it favored biomass accumulation and increased stem density in plants under shade.

4. The plant growth regulators disturbed the biomass allocation among root, stem, and leaf. Gibberellin promoted allocation to stem replacing leaf biomass; trinexapac-ethyl promoted root replacing stem and leaf biomass; mepiquat and chlormequat chloride promoted stem in detriment of leaf biomass.

ACKNOWLEDGEMENTS

To Terasol Oleos Vegetais for financial support (Project SEG 30.20.90.020.00.00) and to Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (PIBIC grant).

LITERATURE CITED

- Balkcom, K. S.; Monks, C. D.; Brown, S. M. Mepiquat chloride applications across two nitrogen rates in a conservation tillage cotton system. *Journal of Cotton Science*, v.26, p.1-13, 2022. <https://doi.org/10.56454/LTOH4319>
- Campbell, D. N.; Rowland, D. L.; Schnell, R. W.; Ferrel, J. A. Developing a castor (*Ricinus communis* L.) production system in Florida, U.S.: evaluating crop phenology and response to management. *Industrial Crops and Products*, v.53, p.217-227, 2014. <https://doi.org/10.1016/j.indcrop.2013.12.035>
- Castro-Camba, R.; Sánchez, C.; Vidal, N.; Vielba, J. M. Plant development and crop yield: the role of gibberellins. *Plants*, v.11, p.1-17, 2022. <https://doi.org/10.3390/plants11192650>
- Chalise, D. P.; Snider, J. L.; Hand, L. C.; Roberts, P.; Vellidis, G.; Ermanis, A.; Collins, G. D.; Lacerda, L. N.; Cohen, Y.; Pokhrel, A.; Parkash, V.; Lee, J. M. Cultivar, irrigation management, and mepiquat chloride strategy: Effects on cotton growth, maturity, yield, and fiber quality. *Field Crops Research*, v.286, p.108633, 2022. <https://doi.org/10.1016/j.fcr.2022.108633>
- Chungloo, D.; Tisarum, R.; Samphumphuang, T.; Sotesaritkul, T.; Cha-Um, S. Regulation of curcuminoids, photosynthetic abilities, total soluble sugar, and rhizome yield traits in two cultivars of turmeric (*Curcuma longa*) using exogenous foliar paclobutrazol. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, v.49, p.1-17, 2021. <https://doi.org/10.15835/nbha49312445>
- Ervin, E. H.; Koski, A. J. Growth responses of *Lolium perenne* L. to trinexapac-ethyl. *HortScience*, v.33, p.1200-1202, 1998. <https://doi.org/10.21273/hortsci.33.7.1200>
- Ferrari, S.; Polycarpo, G. V.; Vargas, P. F.; Fernandes, A. M.; Cunha, M. L. O.; Pagliari, P. Mix of trinexapac-ethyl and nitrogen application to reduce upland rice plant height and increase yield. *Plant Growth Regulation*, v.96, p.209-219, 2022. <https://doi.org/10.1007/s10725-021-00770-0>
- Giertych, M. J.; Karolewski, P.; Oleksyn, J. Carbon allocation in seedlings of deciduous tree species depends on their shade tolerance. *Acta Physiologiae Plantarum*, v.37, p.1-15, 2015. <https://doi.org/10.1007/s11738-015-1965-x>
- Hadi, F.; Ahmad, A.; Ullah, R. Cadmium phytoextraction potential of *Ricinus communis* significantly increased with exogenous application of growth regulators and macronutrients. *Soil and Sediment Contamination: An International Journal*, v.30, p.663-685, 2021. <https://doi.org/10.1080/15320383.2021.1885345>
- Islam, M. S.; Hasan, M. K.; Islam, B.; Renu, N. A.; Hakim, M. A.; Islam, M. R.; Chowdhury, M. K.; Ueda, A.; Saneoka, H.; Ali Raza, M.; Fahad, S.; Barutçular, C.; Çig, F.; Erman, M.; El Sabagh, A. Responses of water and pigments status, dry matter partitioning, seed production, and traits of yield and quality to foliar application of GA3 in mungbean (*Vigna radiata* L.). *Frontiers in Agronomy*, v.2, p.1-17, 2021. <https://doi.org/10.3389/fagro.2020.596850>
- Jiao, X.; Zhi, W.; Liu, G.; Zhu, G.; Feng, G.; Ahmed Nimir, N. E.; Ahmad, I.; Zhou, G. Responses of foreign GA3 application on seedling growth of castor bean (*Ricinus communis* L.) under salinity stress conditions. *Agronomy*, v.9, p.1-13, 2019. <https://doi.org/10.3390/agronomy9060274>

- Kalbfuß, N.; Strohmayer, A.; Kegel, M.; LE, L.; Grosse-Holz, F.; Brunschweiler, B.; Stöckl, K.; Wiese, C.; Franke, C.; Schiestl, C.; Prem, S.; Sha, S.; Franz-Oberdorf, K.; Hafermann, J.; Thiemé, M.; Facher, E.; Palubicki, W.; Bolle, C.; Assaad, F. F. A role for brassinosteroid signalling in decision-making processes in the *Arabidopsis* seedling. *PLoS Genetics*, v.18, p.1-31, 2022. <https://doi.org/10.1371/journal.pgen.1010541>
- Kupke, B. M.; Tucker, M. R.; Able, J. A.; Porker, K. D. Manipulation of barley development and flowering time by exogenous application of plant growth regulators. *Frontiers in Plant Science*, v.12, p.1-15, 2022. <https://doi.org/10.3389/fpls.2021.694424>
- Matos, F. S.; Freitas, I. A. S.; Pereira, V. L. G.; Pires, W. K. L. Effect of gibberellin on growth and development of *Spondias tuberosa* seedlings. *Revista Caatinga*, v.33, p.1124-1130, 2020. <https://doi.org/10.1590/1983-21252020v33n427rc>
- Mehmood, M. Z.; Qadir, G.; Afzal, O.; Din, A. M. U.; Raza, M. A.; Khan, I.; Hassan, M. J.; Awan, S. A.; Ahmad, S.; Ansar, M.; Aslam, M. A.; Ahmed, M. Paclobutrazol improves sesame yield by increasing dry matter accumulation and reducing seed shattering under rainfed conditions. *International Journal of Plant Production*, v.15, p.337-349, 2021. <https://doi.org/10.1007/s42106-021-00132-w>
- Oswalt, J. S.; Rieff, J. M.; Severino, L. S.; Auld, D. L.; Bednarz, C. W.; Ritchie, G. L. Plant height and seed yield of castor (*Ricinus communis* L.) sprayed with growth retardants and harvest aid chemicals. *Industrial Crops and Products*, v.61, p.272-277, 2014. <https://doi.org/10.1016/j.indcrop.2014.07.006>
- Pricinotto, L. F.; Zucareli, C. Paclobutrazol on growth and yield performance of soybean under different plant densities. *Revista Caatinga*, v.27, p.65-74, 2014.
- Qi, H.-K.; Du, M.-W.; Meng, L.; Xie, L.-W.; Eneji, A. E.; Xu, D.-Y.; Tian, X.-L.; Li, Z.-H. Cotton maturity and responses to harvest aids following chemical topping with mepiquat chloride during bloom period. *Journal of Integrative Agriculture*, v.21, p.2577-2587, 2022. <https://doi.org/10.1016/j.jia.2022.07.008>
- Severino, L. S. Plants make smart decisions in complex environments. *Plant Signaling and Behavior*, v.16, p.1-14, 2021. <https://doi.org/10.1080/15592324.2021.1970448>
- Severino, L. S. Single-seed selection of fast-germinating genotypes of castor (*Ricinus communis*). *Industrial Crops and Products*, v.194, p.116307, 2023a. <https://doi.org/10.1016/j.indcrop.2023.116307>
- Severino, L. S. Plant height and biomass of castor plants treated with plant growth regulators, Redape, 2023b.
- Shifriss, O. Gibberellin as sex regulator in *Ricinus communis*. *Science*, v.133, p.2061-2062, 1961. <https://doi.org/10.1126/science.133.3470.2061>
- Souza, I. L.; Da Silva, T. R. B.; Albrecht, L. P. Management of trinexapac-ethyl application in soybean. *Nativa*, v.10, p.16-21, 2022. <https://doi.org/10.31413/nativa.v10i1.12749>
- Souza-Schlick, G. D.; Soratto, R. P.; Fernandes, A. M.; Martins, J. D. L. Mepiquat chloride effects on castor growth and yield: Spraying time, rate, and management. *Crop Science*, v.58, p.880-891, 2018. <https://doi.org/10.2135/cropsci2017.07.0420>
- Teixeira, A. G.; Parajara, M. D. C.; Oliveira, F. L.; Zucoloto, M.; Dalvi, L. P. Ornamental cauliflower production using growth regulator. *Horticultura Brasileira*, v.40, p.76-81, 2022. <https://doi.org/10.1590/s0102-0536-20220110>
- Umaña, M. N.; Cao, M.; Lin, L.; Swenson, N. G.; Zhang, C. Trade-offs in above- and below-ground biomass allocation influencing seedling growth in a tropical forest. *Journal of Ecology*, v.109, p.1184-1193, 2021. <https://doi.org/10.1111/1365-2745.13543>
- Witchard, M. Paclobutrazol is phloem mobile in castor oil plant (*Ricinus communis* L.). *Journal of Plant Growth Regulation*, v.16, p.215-217, 1997. <https://doi.org/10.1007/PL00006999>
- Zhou, G.; Nimir, N.; Lu, S.; Zhai, F.; Wang, Y. Gibberellic acid and salinity affected growth and antioxidant enzyme activities in castor bean plants at early growth stage. *Agronomy Journal*, v.106, p.1340-1348, 2014. <https://doi.org/10.2134/agronj14.0044>