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Growth and Tuber Yield of Go Potato 'Medians' in Response to Cytokinin and Prohexadione-Ca Application Frequency at Medium Altitude

Sahrul Ramdhani[1]*, Rahmat Budiarto[2], Arya Widyawan[3], Supatida Abdullakasim[4], Jajang Sauman Hamdani[2]

[1] Study Program of Master of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Sumedang, Indonesia
[2] Department of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Sumedang, Indonesia
[3] College of Food and Agriculture Sciences, King Saud University, Riyadh 11451, Saudi Arabia
[4] Department of Horticulture, Faculty of Agriculture at Kamphaeng Saen, Kasetsart University, Nakhon Patom, Thailand

*Correspondence E-mail: jajang.sauman@unpad.ac.id

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ABSTRACT

Background: G_0 potato seed production at medium altitude is constrained by high temperatures that may promote gibberellin-mediated vegetative growth and inhibit tuber formation.
Aims: This study aimed to evaluate the interaction between cytokinin and prohexadione-Ca application frequencies and determine suitable frequencies for improving the growth and yield of G_0 potato cultivar 'Medians'.
Methods: The experiment was conducted in a screenhouse in Garut, Indonesia, at approximately 706 m above sea level, using a factorial randomized complete block design (RCBD) with three replications. Cytokinin was applied once (28 days after planting), twice (28 and 35 days), or three times (28, 35, and 42 days), whereas prohexadione-Ca was applied once (49 days), twice (49 and 56 days), or three times (49, 56, and 63 days).
Results: A significant interaction was observed for the number of stolons and percentage of L-class tubers. Three cytokinin applications combined with three prohexadione-Ca applications produced the highest number of stolons (30.78 stolons per plant), whereas three cytokinin applications combined with two prohexadione-Ca applications produced the highest percentage of L-class tubers (24.74%). Independently, three cytokinin applications produced the highest leaf area (1,241.64 cm^2), leaf area index (0.927), and number of tubers per plant (15.15). Two prohexadione-Ca applications produced the highest plant dry weight (30.46 g), number of tubers per plant (12.96), and yield per plant (77.91 g), while increasing tuber growth rate and harvest index to levels statistically comparable to those obtained with three applications.
Conclusion: These findings indicate that two prohexadione-Ca applications were most effective for improving tuber production, whereas three cytokinin applications maximized tuber number under medium-altitude conditions.

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1. Introduction

Potato is an important annual vegetable crop that plays a significant role in supporting food diversification. Haverkort *et al.* (2023) stated that potato has the potential to serve as a non-rice carbohydrate source and contains vitamin C and potassium, which provide health benefits. In addition to being consumed directly, potato is widely used as a raw material for various processed products, such as chips, French fries, and potato flour (Fleming & Morris, 2024). Potato demand continues to increase along with population growth and the development of the food industry. PUSDATIN (2023) reported that average national potato consumption in 2022 reached 2.27 kg capita^{-1} year^{-1}, representing a 3.2% increase compared with the previous year. Meanwhile, BPS (2023) indicated that the increase in potato production has not been sufficient to keep pace with the growth in national consumption. This condition highlights the need for effective and sustainable strategies to increase potato production.

Increasing potato production through the development of highland areas faces several constraints. Husen *et al.* (2023) reported that potato intensification in highland areas can be constrained by soil-borne diseases, such as the potato cyst nematode. Meanwhile, Supriatna *et al.* (2018) stated that potato expansion in highland areas is limited by erosion risks and the presence of protected areas. Therefore, medium-altitude areas represent a strategic alternative for expanding potato production. Mubarok *et al.* (2022) demonstrated that potato cultivation at medium altitude can support increased production, particularly when accompanied by appropriate cultivation technologies. One cultivar with potential for cultivation under these conditions is 'Medians', which has been reported to adapt to daytime temperatures of up to 28°C and produce higher tuber numbers and larger tuber diameters than other cultivars (Supriatna *et al.,* 2018).

The development of potato production at medium altitude needs to be supported by the availability of high-quality seed. G_0 (Generation 0) potato seed is basic seed produced from mini-tubers derived from tissue-culture plantlet cuttings and possesses high genetic and physiological quality with relatively low pathogen contamination (Mulyono *et al.,* 2017). Sembiring *et al.* (2021) explained that the use of G_0 seed plays an important role in producing productive and healthy subsequent seed generations, thereby supporting the sustainability of the potato seed production system. Therefore, G_0 potato seed production at medium altitude is important for increasing the availability of high-quality seed outside the main production zones in highland areas.

Despite its potential, G_0 potato seed production at medium altitude still faces the challenge of relatively high temperatures. Hamdani *et al.* (2017) explained that high temperatures can increase gibberellin activity, promote vegetative growth, delay tuber formation, and reduce assimilate translocation to storage organs. Beck *et al.* (2026) also reported that high temperature is one of the environmental factors that restrict potato tuber formation and bulking. In addition, disruption of the source–sink relationship under high-temperature conditions may be associated with reduced photo assimilate mobilization and decreased activity of enzymes involved in starch accumulation in tubers (Sánchez-correa *et al.,* 2024). Therefore, a physiological approach is needed to regulate the balance among vegetative growth, stolon formation, and tuber filling in potatoes cultivated at medium altitude.

The application of plant growth regulators (PGRs) is one strategy for regulating the balance between vegetative growth and tuber formation. Cytokinin play important roles in cell division, leaf expansion, and lateral shoot development (Kaur *et al.,* 2022). In potato, cytokinin are also involved in the formation of lateral organs such as stolons; therefore, their application during the early growth stage has the potential to enhance the development of the initial source and sink. According to Danilova *et al.* (2022) cytokinin may regulate chlorophyll degradation and physiological processes associated with starch biosynthesis in stolon tissues. Thus, cytokinin application during the early growth stage is expected to support canopy development, stolon formation, and plant readiness to enter the tuber formation phase.

Following the development of the canopy and initial stolons, potato plants enter the tuber initiation and bulking phases. During these phases, active gibberellin activity needs to be controlled to prevent excessive vegetative growth and promote greater assimilate allocation to storage organs. Diwan *et al.* (2022) stated that prohexadione-Ca is a growth retardant that inhibits the biosynthesis of active gibberellins at the final stage of the pathway. A reduction in active gibberellin levels can suppress stem and stolon elongation, accelerate stolon differentiation into tubers, and increase photo assimilate allocation to storage organs (Castro-camba *et al.,* 2022). In addition, Hernawati *et al.* (2025) reported that prohexadione-Ca has the advantage of relatively rapid degradation and may promote the accumulation of phenolic compounds in plants. Therefore, prohexadione-Ca has the potential to redirect potato growth from vegetative dominance toward tuber formation and bulking.

The effectiveness of plant growth regulators is determined not only by their type and concentration but also by the timing and frequency of application. Ramadhani *et al.* (2024) explained that regulating the application of growth retardants can affect potato growth and yield under medium-altitude conditions. Hamdani *et al.* (2021) reported that plant responses to growth regulators are strongly influenced by the balance of endogenous hormones and the physiological stage of the plant. Synchronizing cytokinin application during the early growth stage with prohexadione-Ca application from tuber initiation to bulking is hypothesized to enhance source capacity, promote stolon formation, suppress excessive vegetative growth, and increase assimilate allocation to tubers. Rademacher (2016) reported that the greatest effects of prohexadione-Ca application are obtained under conditions of active shoot growth. Therefore, this study was conducted to analyze the effect of cytokinin and prohexadione-Ca application frequencies on the growth and yield of G_0 potato tuber at medium altitude.

2. Methods

The study was conducted in a screenhouse at PT. Horti Agro Makro, Sukaratu Village, Banyuresmi District, Garut Regency, West Java, Indonesia, at an altitude of approximately 706 m above sea level, from August to December. The planting material consisted of 14-days-old potato plantlet cuttings of the 'Medians' cultivar. The growing medium consisted of a mixture of cocopeat + rice husk charcoal + composted chicken manure (1:1:1, v/v/v). The combination of cocopeat and rice husk charcoal was selected to provide complementary water-retention and aeration properties, as supported by Mubarok *et al.* (2027), while composted chicken manure was incorporated as an organic nutrient source. Supporting materials included NPK 16-16-16 fertilizer and pesticides applied according to crop conditions. The main equipment included polybags, a hand sprayer, a thermohygrometer, a leaf porometer (Decagon SC-1), a chlorophyll content meter (Apogee CCM-200 plus), an oven, and a digital balance.

Air temperature and relative humidity inside the screenhouse were monitored using a thermohygrometer. Both parameters were recorded daily at 07:00, 12:00, and 16:00 Western Indonesian Time (WIB). Daily mean values were calculated using a weighted average, assigning twice the weight to the morning observation, while midday and afternoon observations were assigned equal weights. The recorded data were subsequently summarized as monthly means to characterize the microclimatic conditions during the observation period.

The experiment used a factorial randomized complete block design (RCBD) with two factors. The first factor was cytokinin application frequency, consisting of once at 28 days after planting (DAP), twice at 28 and 35 DAP, and three times at 28, 35, and 42 DAP. The second factor was prohexadione-Ca application frequency, consisting of once at 49 DAP, twice at 49 and 56 DAP, and three times at 49, 56, and 63 DAP. Each treatment combination was replicated three times, with six plants per experimental unit, resulting in a total of 162 plants. Of the six plants in each experimental unit, two were used for destructive sampling at 50 DAP, two at 75 DAP, and the remaining two were harvested at 93 DAP.

The growing medium was prepared by thoroughly mixing cocopeat, rice husk charcoal, and compost, followed by the application of nematicide at 6 g m^{-2} and disinfectant at 0.5 mL L^{-1}. The growing medium

was placed in 20 cm × 20 cm polybags to half of their capacity. The polybags were arranged with a spacing of 20 cm between adjacent polybags. Plantlet cuttings were planted in the center of each polybag, with three nodes retained from the shoot apex and an approximate cutting length of 5 cm. During the early growth stage, the plants were covered with shading net to reduce direct light exposure and the risk of wilting. The shading net is opened when the plants are 14 DAP.

Crop maintenance included irrigation, fertigation, supplementary fertilization, hilling, staking, and pest and disease management. Plants were irrigated twice daily, while fertigation was applied daily from 5 to 80 DAP using NPK 16-16-16 at a concentration of 1 g L^{-1}, with 50 mL applied per plant. Supplementary fertilization was performed using 2 g of NPK 16-16-16 per plant at 1 and 4 weeks after planting (WAP). Hilling was performed during the second supplementary fertilization (4 WAP) until the polybags were completely filled with growing medium. Bamboo stakes measuring 75 cm in length were used to support the plants. Pest and disease management was conducted weekly or adjusted according to crop conditions.

Cytokinin was applied as 6-benzylaminopurine (BAP) at a concentration of 50 ppm, prepared by diluting 50 mL of a 1,000 ppm stock solution (Esha Flora) with water to a final volume of 1 L. Prohexadione-Ca was applied at a concentration of 100 ppm active ingredient, prepared by dissolving 1 g of a commercial formulation containing 10% prohexadione-Ca (Pordeex) in water to obtain a final spray volume of 1 L. Both plant growth regulators were applied uniformly to the foliage using a hand sprayer. Cytokinin was applied at 15 mL per plant during the first and second applications and 20 mL per plant during the third application, whereas prohexadione-Ca was applied at 20 mL per plant during the first application and 25 mL per plant during the second and third applications.

Observations included growth and yield parameters. Plant height was measured at 75 days after planting (DAP) using three sample plants per experimental unit. Leaf area was determined at 75 DAP using the gravimetric method described by Sitompul & Guritno, (1995). Fifteen circular leaf discs with a radius of 0.3 cm were collected from randomly selected leaves. Leaf area was calculated as follows:

$$\text{Leaf Area} = \frac{\text{TLW}}{\text{DLS}} \text{ x n x } \pi \text{ x } r^2 \text{ cm}^2$$

where TLW represents total leaf dry weight per plant, DLS represents the combined dry weight of the sampled leaf discs, n represents number of circular leaf discs (15) and r represents the disc radius. Leaf area index was calculated by dividing leaf area by the growing area per plant.

Chlorophyll content index and stomatal conductance were measured at 73 DAP on three plants per experimental unit, using three fully expanded, non-senescent leaves per plant (the third, fourth, and fifth leaves from the shoot apex). These leaves were selected because they were physiologically active and had not entered the senescence stage (Taiz *et al.,* 2015). Chlorophyll content index and stomatal conductance was measured between 08:00 and 10:00 WIB, to minimize the influence of environmental variability on physiological measurements. Stomatal conductance was measured on the abaxial leaf surface using a leaf porometer. The abaxial surface was selected based on the distribution and physiological function of stomata (Sultana *et al.,* 2024). Morning measurements were conducted to minimize environmental variability affecting stomatal activity (Potkay & Feng, 2023). The number of shoots was recorded at 75 DAP using three sample plants per experimental unit.

Net assimilation rate and relative growth rate were calculated from destructive samples collected at 50 and 75 DAP, with two plants sampled per experimental unit at each observation time. Net assimilation rate, which represents the rate of dry matter accumulation per unit leaf area over time (Li *et al.,* 2016), was calculated as follows:

$$\text{Net Assimilation Rate} = \frac{(W2-W1)}{(T2-T1)} \text{ x } \frac{(\text{LnA2}-\text{LnA1})}{(A2-A1)} \text{ g cm}^{-2}\text{day}^{-1}$$

Relative growth rate, which represents the rate of biomass accumulation relative to existing biomass (Rees *et al.,* 2010), was calculated as follows:

$$\text{Relative Growth Rate} = \frac{(W2-W1)}{(T2-T1)} \text{ x } \frac{(LnA2-LnA1)}{(A2-A1)} \text{ g cm}^{-2}\text{day}^{-1}$$

where W represents total plant dry weight, LA represents leaf area, and T represents time. Subscripts 1 and 2 indicate measurements at 50 and 75 DAP, respectively. The shoot-to-root ratio was calculated at 75 DAP by dividing shoot dry weight by root dry weight to characterize biomass allocation between aboveground and belowground plant organs (Poorter *et al.,* 2012). Plant dry weight was determined by oven-drying the destructively sampled plant material at 80 °C for 48 h.

Tuber growth rate was calculated from changes in tuber dry weight between 50 and 75 DAP, using the following equation:

$$\text{Tuber Growth Rate} = \frac{(TW_2 - TW_1)}{(T2-T1)} \text{ g day}^{-1}$$

where TW represents tuber dry weight, and subscripts 1 and 2 indicate measurements at 50 and 75 DAP, respectively. Harvest index was calculated as the ratio of tuber dry weight to total plant dry weight, following the approach cited by Khan *et al.,* (2014):

$$\text{Harvest Index} = \frac{\text{Tuber dry weight}}{\text{Total plant dry weight}}$$

Yield observations were conducted on the two remaining plants per experimental unit at harvest (93 DAP), when the plants exhibited physiological signs of maturity, characterized by yellowing leaves, dried stems, and tuber skins that were not easily peeled. The number of stolons was determined by counting the stolons on each sampled plant. The percentage of stolons forming tubers was calculated as follows:

$$\text{Stolons Forming Tubers} = \frac{\text{Number of tuber} - \text{bearing stolons}}{\text{Total number of stolons}} \text{ x } 100\ \%$$

Tuber yield per plant was determined from the total fresh weight of harvested tubers at 93 DAP. The number of tubers per plant was determined by counting all harvested tubers, regardless of size class. Tubers were classified according to the G_0 potato seed classification established by the Indonesian Ministry of Agriculture (Kementerian Pertanian, 2015), namely S (<5 g), M (5–20 g), and L (>20 g). The percentage of tubers in each size class was calculated as follows:

$$\text{Tuber Size Class} = \frac{\text{Number of tubers in the corresponding size class}}{\text{Total number of tubers per plant}} \text{ x } 100\ \%$$

The data were subjected to analysis of variance (ANOVA) based on the factorial RCBD model at the 5% significance level. When the ANOVA indicated a significant treatment effect, the analysis was followed by Duncan's Multiple Range Test (DMRT) at the 5% significance level. Statistical analyses were performed using Microsoft Excel with the SmartstatXL V.3.6.5.4 add-in.

3. Results and Discussion

3.1 Environmental Conditions

The microclimatic conditions inside the screenhouse were characterized by high air temperatures during the observation period. As presented in Table 1, monthly mean daily temperatures ranged from 36.9°C to 39.4°C, with the highest value recorded in October and the lowest in December 2024. Midday temperatures reached 43.3–45.1°C, exceeding the favorable temperature range for potato growth and tuber development (Trapero-mozos *et al.,* 2018). Elevated temperatures can impair potato photosynthetic performance and reduce the accumulation of assimilates required for tuber development (Muthoni & Shimelis, 2020). High-temperature conditions may also alter assimilate partitioning between vegetative organs and developing tubers, potentially restricting tuber growth (Sánchez-correa *et al.,* 2024).

Table 1. Mean daily air temperature and relative humidity during the experimental period

Month	Temperature (°C)				Relative Humidity (%)			
	Morning	Midday	Afternoon	Daily Mean	Morning	Midday	Afternoon	Daily Mean
October	36.3	45.1	39.6	39.4	73.6	62.2	77.3	71.7
November	34.3	44.3	40.0	38.2	72.6	60.7	72.8	69.7
December	33.5	43.3	37.3	36.9	74.1	60.9	75.8	71.2

Monthly mean relative humidity ranged from 69.7% to 71.7%, with lower values consistently recorded at midday (Table 1). The decline in relative humidity during the hottest part of the day may increase atmospheric evaporative demand and influence plant water relations (Zahra *et al.,* 2023). Stomatal conductance may also regulated by environmental conditions and plant water status, which influence gas exchange and transpiration (Lawson & Matthews, 2020). This observed microclimatic conditions provide an important physiological context for interpreting the growth and tuber yield responses of G_0 potato plants to cytokinin and prohexadione-Ca application frequencies.

3.2 Overview of ANOVA Results for Growth and Yield Parameters

The interaction between cytokinin and prohexadione-Ca application frequencies did not significantly affect most of the observed parameters, except for the number of stolons and the percentage of L-class tubers (Table 2). This pattern indicates that both PGR factors primarily elicited independent responses, consistent with their distinct physiological mechanisms. Cytokinin primarily regulate cell division, meristem activity, and source–sink organ development (Ruan & Yi, 2022), whereas prohexadione-Ca inhibits gibberellin biosynthesis, thereby modifying plant architecture and assimilate allocation (Teixeira *et al.,* 2021). The interactions observed for the number of stolons and the percentage of L-class tubers indicate that the combined effects of the two PGRs may become more important during the formation and bulking of storage organs.

Table 2. Summary of the effects of cytokinin and prohexadione-Ca application frequencies on each observed parameter

Observed parameter	Cytokinin	Prohexadione-Ca	Cytokinin x Prohexadione-Ca
Plant height (cm)	ns	*	ns
Leaf area (cm^2 $plant^{-1}$)	*	ns	ns
Leaf area index	*	ns	ns
Chlorophyll content index	ns	ns	ns
Stomatal conductance (µmol H_2O m^{-2} s^{-1})	ns	ns	ns
Number of lateral shoots (shoots $plant^{-1}$)	*	*	ns
Plant dry weight (g $plant^{-1}$)	*	*	ns
Net assimilation rate (g cm^{-2} day^{-1})	*	*	ns
Relative growth rate (g g^{-1} day^{-1})	ns	*	ns
Tuber growth rate (g day^{-1})	*	*	ns
Shoot-root ratio	ns	ns	ns
Harvest index	ns	*	ns
Number of stolons (stolons $plant^{-1}$)	*	*	*
Number of tubers per plant (tubers $plant^{-1}$)	*	*	ns
Stolons forming tubers (%)	*	*	ns
Yield per plant (g $plant^{-1}$)	*	*	ns

S-class tubers (%)	ns	ns	ns
M-class tubers (%)	*	ns	ns
L-class tubers (%)	*	*	*

*Description: ns = not significantly different; * = significantly different at the 5% level.*

In general, cytokinin affected parameters associated with canopy development and source capacity, including leaf area, leaf area index, number of shoots, plant dry weight, net assimilation rate, tuber growth rate, number of stolons, percentage of stolons forming tubers, number of tubers, and yield per plant. In contrast, prohexadione-Ca primarily affected plant height, relative growth rate, harvest index, and various yield components. This pattern may indicate a differentiation in the physiological functions of the two PGRs, with cytokinin playing a greater role in the formation and maintenance of source tissues (Thapa et al., 2024), whereas prohexadione-Ca regulates vegetative growth by inhibiting gibberellin biosynthesis (Hernawati et al., 2022).

3.3 Growth Responses

3.3.1 Plant Height, Leaf Area, and Leaf Area Index

There was no significant interaction between cytokinin and prohexadione-Ca application frequencies on plant height, leaf area, or leaf area index (Table 2). Prohexadione-Ca application frequency significantly affected plant height but not leaf area or leaf area index (Table 3). Three applications significantly reduced plant height to 45.44 cm compared with 53.67 cm following a single application, whereas two applications (49.61 cm) did not differ significantly from either treatment. This reduction may be attributed to the inhibition of gibberellin biosynthesis by prohexadione-Ca through 2-oxoglutarate-dependent dioxygenases, particularly those involved in the conversion of GA20 to GA1 and GA9 to GA4 (Kim *et al.,* 2019; Rademacher, 2016). Reduced active gibberellin levels restrict stem cell elongation, resulting in shorter plants. The greater reduction following three applications suggests that repeated treatments may prolong the suppression of gibberellin-mediated stem elongation without significantly altering leaf canopy development. Cytokinin application frequency significantly affected leaf area and leaf area index (Figure 1), but not plant height (Table 3). Leaf area increased significantly with each additional application, reaching 1,241.64 cm^2 after three applications. However, leaf area index increased significantly only after three applications (0.927), whereas two applications (0.788) did not differ significantly from a single application (0.684). These responses may be attributed to the role of cytokinin in promoting cell division and leaf development, thereby increasing photosynthetic surface area (Wu *et al.,* 2021). Cytokinin also contributes to maintaining chloroplast integrity and photosynthetic function (Rodrigues *et al.,* 2025). Similar findings were reported by Nuraini *et al.* (2021), who observed increased leaf area in potato following cytokinin application without a consistent effect on plant height.

Table 3. Independent effects of cytokinin and prohexadione-Ca application frequencies on plant height, leaf area, and leaf area index

Treatment	Plant height (cm)	Leaf area (cm^2)	Leaf area index
Cytokinin application frequency:			
Once (28 DAP)	49.56 a	849.61 a	0.684 a
Twice (28 and 35 DAP)	50.19 a	1,010.74 b	0.788 a
Three times (28, 35, and 42 DAP)	48.97 a	1,241.64 c	0.927 b
Prohexadione-Ca application frequency:			
Once (49 DAP)	53.67 b	989.82 a	0.796 a
Twice (49 and 56 DAP)	49.61 ab	1,101.59 a	0.842 a
Three times (49, 56, and 63 DAP)	45.44 a	1,010.58 a	0.761 a

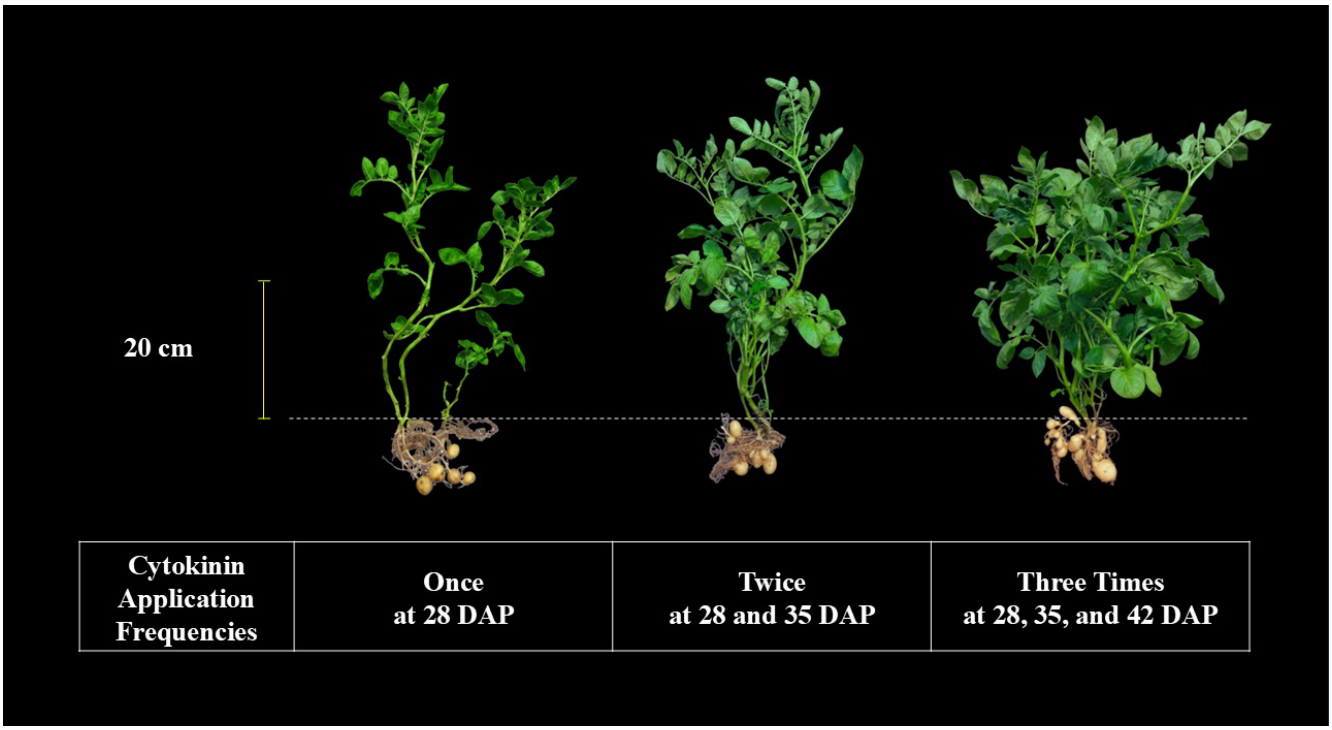

Figure 1. Leaf area index significantly increased as the increase of cytokinin application frequency

3.3.2 Chlorophyll Content Index, Stomatal Conductance, and Number of Lateral Shoots

There was no significant interaction effect between cytokinin and prohexadione-Ca application frequencies on the chlorophyll content index, stomatal conductance, and number of lateral shoots (Table 2). Additionally, chlorophyll content index was not affected by the application frequency of either PGR (Table 4). This finding indicates that this parameter was relatively insensitive to repeated applications under the conditions of the present study. Hernawati *et al.* (2022) reported that prohexadione-Ca at 50 ppm increased chlorophyll content index, whereas application timing at 30, 40, and 50 DAP had no significant effect. Thus, chlorophyll responses may be determined more strongly by PGR concentration and leaf physiological status than by application frequency or timing alone. This stability may also be associated with the maintenance of chloroplast integrity and adequate leaf nitrogen status (Fernandes *et al.,* 2021). In addition to plant growth regulators, chlorophyll content may also be influenced by environmental factors, particularly light conditions. Sobari *et al.* (2026) reported significantly higher total chlorophyll content in strawberry plants under natural (non-LED) lighting (0.26 mg g^{-1}) than under supplemental LED lighting (0.20 mg g^{-1}).

Table 4. Independent effects of cytokinin and prohexadione-Ca application frequencies on the chlorophyll content index, stomatal conductance, and number of lateral shoots

Treatment	Chlorophyll content index	Stomatal conductance (µmol H_2O m^{-2} s^{-1})	Number of lateral shoots
Cytokinin application frequency:			
Once (28 DAP)	30.00 a	432.12 a	3.19 a
Twice (28 and 35 DAP)	29.76 a	399.49 a	4.33 b
Three times (28, 35, and 42 DAP)	30.00 a	461.50 a	4.74 b
Prohexadione-Ca application frequency:			
Once (49 DAP)	30.00 a	433.18 a	3.00 a

Twice (49 and 56 DAP)	30.01 a	417.80 a	4.30 b
Three times (49, 56, and 63 DAP)	29.75 a	442.12 a	4.96 c

Description: Means followed by the same letter in the same column for each factor are not significantly different according to Duncan's multiple range test at the 5% level.

Stomatal conductance also did not differ significantly among cytokinin or prohexadione-Ca application frequencies (Table 4). This finding indicates that differences in application frequency were insufficient to significantly modify stomatal responses. Stomatal conductance is more strongly influenced by leaf hydraulic status, vapor pressure deficit (VPD), and abscisic acid (ABA) signaling than by hormonal changes induced by PGR treatments (Bourbia & Brodribb, 2024; Lawson & Matthews, 2020). This finding is consistent with Hernawati *et al.* (2022) who reported that stomatal conductance was more responsive to environmental conditions and PGR concentration than to application timing.

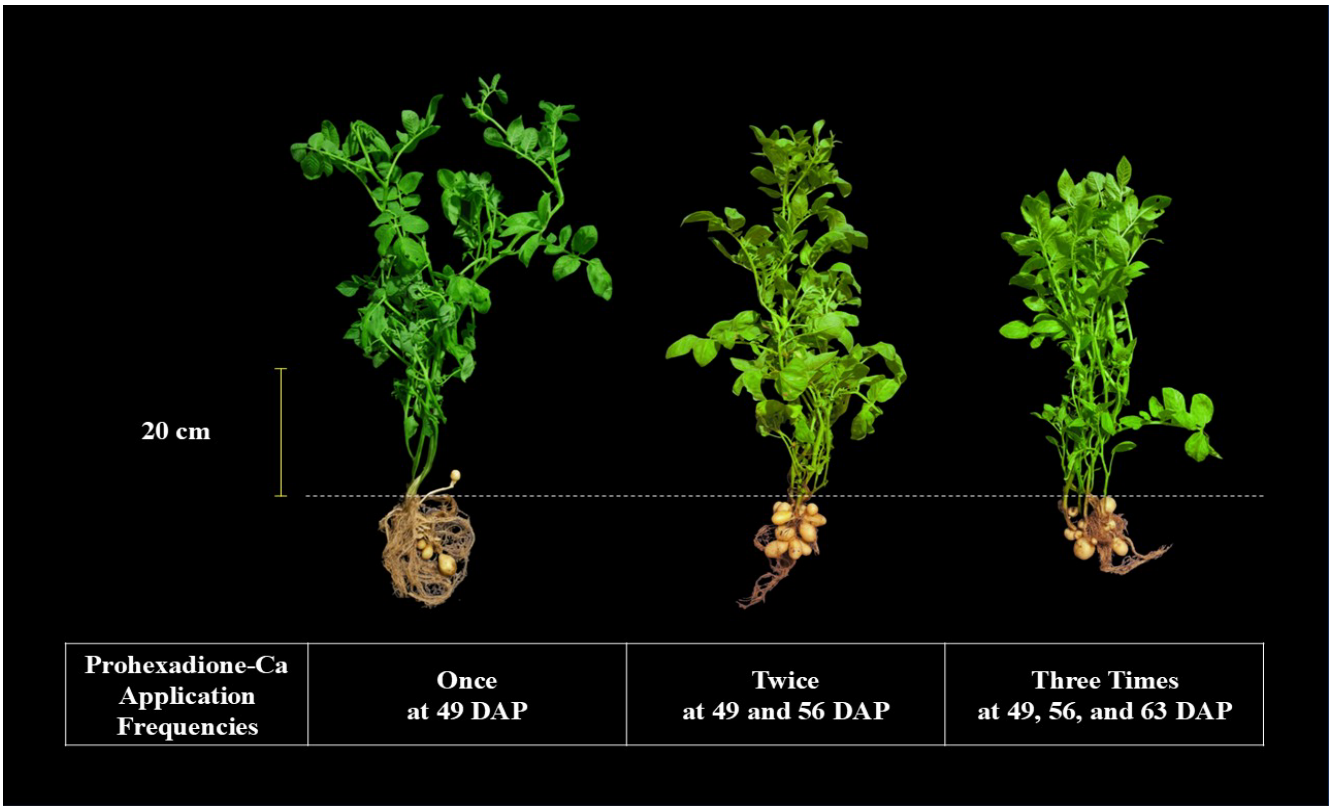

Figure 2. Plant height significantly decreased, while lateral shoot number significantly increase as the increase of prohexadione-Ca application frequencies

In contrast, the increase of application frequency of both cytokinin and prohexadione-Ca significantly increased the number of lateral shoots, but the response patterns differed between the two PGRs (Table 4). Cytokinin application reached a maximum response with two applications, which was not significantly different from three applications, whereas the number of lateral shoots continued to increase with increasing prohexadione-Ca application frequency, reaching the highest value with three applications (Figure 2). Cytokinins stimulate meristematic cell division and axillary bud activation through cytokinin response regulator pathways (Kaur *et al.,* 2022). Meanwhile, prohexadione-Ca reduces apical dominance by inhibiting gibberellin biosynthesis, thereby promoting lateral shoot development (Lal *et al.,* 2022). These mechanisms are consistent with Mubarok *et al.* (2022), who described the role of cytokinins in cell division and sink activity, as well as the role of growth retardants in suppressing gibberellin biosynthesis.

3.3.3 Net assimilation rate, relative growth rate, and shoot-to-root ratio

Net assimilation rate (NAR) was independently affected by both PGRs (Table 5). Cytokinin application increased NAR up to two applications but decreased with the third application, whereas prohexadione-Ca resulted in the highest NAR with three applications, reaching 0.000646 g cm^{-2} day^{-1}. Cytokinins can enhance photosynthetic efficiency by maintaining chloroplast function; however, excessive stimulation may reduce net efficiency by increasing maintenance respiration requirements (Danilova *et al.,* 2022). Prohexadione-Ca may improve assimilation efficiency by restricting elongation growth and altering carbon allocation toward biomass production (Zhang *et al.,* 2023).

Table 5. Independent effects of cytokinin and prohexadione-Ca application frequencies on the net assimilation rate, relative growth rate, and shoot-to-root ratio

Treatment	Net assimilation rate (g cm^{-2} day^{-1})	Relative growth rate (g g^{-1} day^{-1})	Shoot-to-root ratio
Cytokinin application frequency:			
Once (28 DAP)	0.000515 a	0.019 a	3.627 a
Twice (28 and 35 DAP)	0.000669 b	0.023 a	4.146 a
Three times (28, 35, and 42 DAP)	0.000488 a	0.021 a	4.372 a
Prohexadione-Ca application frequency:			
Once (49 DAP)	0.000518 a	0.020 a	4.106 a
Twice (49 and 56 DAP)	0.000509 a	0.018 a	4.128 a
Three times (49, 56, and 63 DAP)	0.000646 b	0.024 b	3.911 a

Description: Means followed by the same letter in the same column for each factor are not significantly different according to Duncan's multiple range test at the 5% level.

Cytokinin application frequency showed no significant main effect on relative growth rate, indicating that repeated applications during the early vegetative phase did not substantially alter relative biomass accumulation. Although cytokinin promotes cell division and shoot development, these physiological responses may not necessarily translate into increased relative growth under the relatively high-temperature conditions of medium-altitude cultivation. Elevated temperatures may increase respiratory carbon losses, thereby limiting net biomass accumulation despite enhanced vegetative activity (Moore *et al.,* 2021). In contrast, prohexadione-Ca application frequency significantly affected relative growth rate, with the highest mean (0.024) observed following three applications. This response may be associated with the inhibition of gibberellin biosynthesis, which restricts excessive shoot elongation and potentially improves the efficiency of biomass accumulation (Rademacher, 2016).

Based on Table 5, neither cytokinin nor prohexadione-Ca application frequency significantly affected the shoot-to-root ratio. The relatively stable response indicates the presence of shoot–root homeostasis that maintained the proportion of carbon allocation despite external hormonal manipulation. Physiologically, this ratio is regulated by the balance between the shoot, which serves as the primary photosynthate-producing organ, and the roots, which function in water and nutrient uptake to support plant growth (Li *et al.,* 2026). Under relatively high temperatures, increased transpiration demand may maintain the importance of root system function; therefore, PGR application was insufficient to significantly shift the balance of carbon allocation between shoots and roots.

3.4 Yield Responses

3.4.1 Plant Dry Weight, Tuber Growth Rate, and Harvest Index

Table 2 showed that there was no significant interaction effect between cytokinin and prohexadione-Ca application frequencies on plant dry weight, tuber growth rate, or harvest index. However, the independent effects of cytokinin and prohexadione-Ca application frequencies significantly affected those parameters, as showed in Table 6.

Table 6. Independent effects of cytokinin and prohexadione-Ca application frequencies on plant dry weight, tuber growth rate, and harvest index

Treatment	Plant dry weight (g plant^{-1})	Tuber growth rate (g day^{-1})	Harvest index
Cytokinin application frequency:			
Once (28 DAP)	23.57 a	0.213 a	0.35 a
Twice (28 and 35 DAP)	28.46 b	0.314 b	0.37 a
Three times (28, 35, and 42 DAP)	28.81 b	0.294 b	0.29 a
Prohexadione-Ca application frequency:			
Once (49 DAP)	24.39 a	0.209 a	0.25 a
Twice (49 and 56 DAP)	30.46 b	0.293 b	0.40 b
Three times (49, 56, and 63 DAP)	25.99 a	0.319 b	0.37 b

Description: Means followed by the same letter in the same column for each factor are not significantly different according to Duncan's multiple range test at the 5% level.

Cytokinin application frequency increased plant dry weight from 23.57 g to 28.46 and 28.81 g with two and three applications, respectively (Table 6). The maximum response observed with two applications suggests that repeated application during leaf development and stolon initiation was able to maintain growth activity and promote the development of early sink organs. Cytokinins also play roles in carbohydrate metabolism and starch synthesis, thereby supporting dry matter accumulation (Mcintyre *et al.,* 2021). In contrast, prohexadione-Ca showed the highest response with two applications, with plant dry weight reaching 30.46 g, followed by a decrease to 25.99 g with three applications. Moderate inhibition of gibberellin biosynthesis may reduce elongation growth and redirect assimilates toward biomass accumulation, whereas excessively frequent applications may potentially restrict the formation of new tissues (Mubarok *et al.,* 2024).

Tuber growth rate increased with twice applications of cytokinin and was not significantly different from that obtained with three applications. Cytokinin supports stolon initiation and sink organ formation through meristematic activity and cell division (Herrera-Isidron *et al.,* 2021). Prohexadione-Ca also produced relatively high responses with two and three applications. Inhibition of gibberellin activity during the early tuberization phase may reduce vegetative dominance and promote carbon allocation to tubers (Bharath & Raju, 2024). The similar response patterns suggest the existence of a physiological optimum beyond which increasing application frequency no longer enhances the rate of tuber biomass accumulation.

Cytokinin application frequency did not significantly affect harvest index, whereas prohexadione-Ca significantly increased harvest index, with the highest value observed with two applications. This finding indicates that cytokinin played a greater role in canopy, shoot, and stolon development, whereas prohexadione-Ca more directly influenced biomass partitioning toward storage organs. Under relatively high-temperature conditions, suppression of gibberellin biosynthesis may reduce shoot dominance and increase carbon allocation to tubers (Hancock *et al.,* 2014; Hernawati *et al.,* 2022).

3.4.2 Number of Stolon

The significant interaction pattern indicates that cytokinin application during stolon initiation (28–42 DAP) and prohexadione-Ca application during the early stolon development phase (49–63 DAP) acted complementarily to increase stolon number (Table 7). Cytokinins are physiologically known to promote cell division and stimulate the formation of lateral organs, such as stolons, through the activation of meristem-related genes, including WUSCHEL and ARR (Herrera-Isidron *et al.,* 2021). Meanwhile, prohexadione-Ca inhibits gibberellin biosynthesis, which otherwise promotes elongation of the main stem, thereby potentially redirecting energy and assimilates toward horizontal growth, including stolon development (Dewi *et al.,* 2024). The combination of both PGRs may extend the stolon formation phase, allowing more stolon primordia to develop before tuberization.

Table 7. Interaction effect of cytokinin and prohexadione-Ca application frequencies on the number of stolons

Cytokinin application frequency	Prohexadione-Ca application frequency		
	Once (49 DAP)	Twice (49 and 56 DAP)	Three times (49, 56, and 63 DAP)
Once (28 DAP)	10.33 a A	12.44 a B	14.56 a C
Twice (28 and 35 DAP)	16.78 b A	18.67 b B	21.33 b C
Three times (28, 35, and 42 DAP)	24.44 c A	26.22 c B	30.78 c C

Description: Means followed by the same letter are not significantly different according to Duncan's multiple range test at the 5% level. Lowercase letters compare cytokinin levels within the same prohexadione-Ca level, while uppercase letters compare prohexadione-Ca levels within the same cytokinin level.

3.4.3 Percentage of Stolons Forming Tubers, Number of Tubers per Plant, and Yield per Plant

Cytokinin and prohexadione-Ca application frequencies independently affected the percentage of stolons forming tubers (Table 8). Cytokinin produced the highest value with two applications, reaching 43.65%, whereas the value decreased to 38.87% with three applications. This response suggests that cytokinin stimulation during 28–35 DAP promoted sink formation, whereas further applications may have maintained vegetative growth and consequently reduced tuberization efficiency (Desta & Amare, 2024). A similar pattern was observed with prohexadione-Ca, indicating that gibberellin inhibition was most effective during the early stolon bulking phase (49–56 DAP), when assimilate allocation to storage organs began to increase. In contrast, the third application at 63 DAP reduced conversion efficiency, potentially because excessive GA inhibition restricted stolon development and consequently reduced tuber formation (Bharath & Raju, 2024).

Table 8. Independent effects of cytokinin and prohexadione-Ca application frequencies on the percentage of stolons forming tubers, number of tubers per plant, and yield per plant

Treatment	Stolons forming tubers (%)	Number of tubers per plant (tubers plant^{-1})	Yield per plant (g plant^{-1})
Cytokinin application frequency:			
Once (28 DAP)	27.24 a	4.81 a	43.62 a
Twice (28 and 35 DAP)	43.65 c	13.70 b	56.34 b

Three times (28, 35, and 42 DAP)	38.87 b	15.15 c	63.35 b
Prohexadione-Ca application frequency:			
Once (49 DAP)	34.20 a	9.30 a	33.51 a
Twice (49 and 56 DAP)	41.13 b	12.96 c	77.91 c
Three times (49, 56, and 63 DAP)	34.43 a	11.41 b	51.89 b

Description: Means followed by the same letter in the same column for each factor are not significantly different according to Duncan's multiple range test at the 5% level.

The number of tubers increased consistently with increasing cytokinin application frequency, from 4.81 to 13.70 and 15.15 tubers per plant with one, two, and three applications, respectively. This increase indicates that repeated cytokinin application during 28–42 DAP enhanced sink formation through stimulation of meristem activity and stolon development. This finding is consistent with Nuraini *et al.* (2021), who explained that cytokinins play important roles in cell division, morphogenesis, shoot formation, and cellular metabolism; thus, their application during the early growth stage can support the development of sink organs in potato. For prohexadione-Ca, the highest number of tubers was obtained with two applications (12.96 tubers per plant), whereas one and three applications produced 9.30 and 11.41 tubers per plant, respectively. This finding indicates that prohexadione-Ca application at 49 and 56 DAP was the most effective frequency for supporting tuber formation. At this stage, the plants had entered the early tuberization and tuber-filling period; therefore, inhibition of gibberellin biosynthesis could reduce vegetative elongation and promote the transition of stolons into tubers. This pattern is consistent with Hernawati *et al.* (2022), who demonstrated that the effectiveness of prohexadione-Ca is strongly influenced by application timing because of its relationship with the stages of stolon and tuber formation.

Tuber yield per plant was significantly affected independently by both factors. Under cytokinin treatment, tuber yield per plant increased from 43.62 g with one application to 56.34 g with two applications and 63.35 g with three applications. However, the two- and three-application treatments did not differ significantly, indicating that increasing cytokinin application frequency from two to three applications did not further increase yield significantly. This finding suggests that cytokinins contribute to early growth capacity and sink formation; however, increases in stolon and tuber numbers are not necessarily accompanied by proportional increases in yield because assimilates must be distributed among a greater number of tubers. This is consistent with Hamdani *et al.* (2021) who explained that tuber number is determined by the number of stolons formed, whereas tuber weight is determined by the amount of photosynthates translocated and stored as reserve materials.

Prohexadione-Ca produced the highest tuber yield with two applications, reaching 77.91 g, compared with 33.51 g with one application and 51.89 g with three applications. This finding indicates that inhibition of gibberellin biosynthesis at 49 and 56 DAP was most effective in directing assimilates toward storage organs. An additional application at 63 DAP did not further optimize yield, suggesting that prolonged inhibition of gibberellin biosynthesis does not necessarily benefit tuber bulking. Ramadhani *et al.* (2024) also reported that prohexadione-Ca can increase tuber number and tuber weight, although its effectiveness strongly depends on the appropriate concentration and application stage. Therefore, two applications of prohexadione-Ca were the most effective treatment for increasing tuber yield per plant under the conditions of this study.

3.4.4 Percentage of Tubers in S, M, and L Size Classes

There was no interaction between the two PGRs for the percentage of S- and M-class tubers (Table 2). Additionally, the percentage of S-class tubers was also not significantly affected by either factor. This finding indicates that the proportion of small tubers was relatively less responsive to application

frequency and was more closely associated with the success of stolon initiation, sink number, and competition among developing tubers (Haverkort & Struik, 2015).

Table 9. Independent effects of cytokinin and prohexadione-Ca application frequencies on the percentage of S- and M-class tubers

Treatment	S-class tubers (%)	M-class tubers (%)
Cytokinin application frequency:		
Once (28 DAP)	34.18 a	65.82 b
Twice (28 and 35 DAP)	46.45 a	34.90 a
Three times (28, 35, and 42 DAP)	39.40 a	42.41 a
Prohexadione-Ca application frequency:		
Once (49 DAP)	43.76 a	46.31 a
Twice (49 and 56 DAP)	39.78 a	45.84 a
Three times (49, 56, and 63 DAP)	36.49 a	50.98 a

Description: Means followed by the same letter in the same column for each factor are not significantly different according to Duncan's multiple range test at the 5% level.

Interestingly, cytokinin significantly affected the percentage of M-class tubers, with the highest proportion observed with one application and lower proportions with repeated applications, whereas prohexadione-Ca had no significant effect. This phenomenon reflects source–sink competition, in which increased leaf area, lateral shoot number, and stolon number resulting from repeated cytokinin applications led to a more divided distribution of assimilates (Oliveira *et al.,* 2021). The reduced efficiency of assimilate translocation at high temperatures further strengthened this effect (Sánchez-correa *et al.,* 2024). Meanwhile, the non-significant effect of prohexadione-Ca indicates that gibberellin inhibition during the bulking phase was not sufficient to modulate size distribution toward M- or S-class tubers, but was more closely related to increasing tuber size toward the larger class (L).

A significant interaction was observed for the percentage of L-class tubers (Table 10). No L-class tubers were produced under any of the once-applied cytokinin treatments, whereas the highest percentage was obtained with the combination of three cytokinin applications and two prohexadione-Ca applications, reaching 24.74%. This finding indicates that repeated cytokinin applications at 28, 35, and 42 DAP enhanced early growth, leaf development, and stolon readiness as potential sink organs, thereby providing a stronger physiological basis for the production of large tubers. This role is consistent with Rohach *et al.* (2023), who explained that cytokinins contribute to cell division, morphogenesis, shoot formation, and the enhancement of early potato growth before tuber formation.

Table 10. Interaction effect of cytokinin and prohexadione-Ca application frequencies on the percentage of L-class tubers

Cytokinin application frequency	Prohexadione-Ca application frequency		
	Once (49 DAP)	Twice (49 and 56 DAP)	Three times (49, 56, and 63 DAP)
Once (28 DAP)	0.00 a A	0.00 a A	0.00 a A
Twice (28 and 35 DAP)	17.38 b A	16.24 b A	22.05 c B
Three times (28, 35, and 42 DAP)	14.29 b A	24.74 c B	15.56 b A

Description: Means followed by the same letter are not significantly different according to Duncan's multiple range test at the 5% level. Lowercase letters compare cytokinin levels within the same prohexadione-Ca level, while uppercase letters compare prohexadione-Ca levels within the same cytokinin level.

Two applications of prohexadione-Ca at 49 and 56 DAP were relatively effective in suppressing gibberellin activity during the early tuber-filling phase, thereby promoting greater assimilate allocation toward tuber enlargement. However, increasing prohexadione-Ca application frequency to three times in combination with three cytokinin applications reduced the percentage of L-class tubers to 15.56%. This pattern indicates that the production of large tubers does not respond linearly to increasing application frequency but depends strongly on the synchronization of application timing with the physiological stage of the plant. Hernawati *et al.* (2022) also reported that the effectiveness of prohexadione-Ca is influenced by application timing because of its relationship with the stages of tuber formation and filling, whereas Ramadhani *et al.* (2024) reported that prohexadione-Ca can support the production of L-class tubers when accompanied by favorable conditions for assimilate accumulation.

4. Conclusions

Cytokinin and prohexadione-Ca application frequencies significantly interacted in determining the number of stolons and the percentage of L-class tubers. Three applications of each plant growth regulator produced the highest observed number of stolons (30.78 stolons per plant), whereas three cytokinin applications combined with two prohexadione-Ca applications produced the highest observed percentage of L-class tubers (24.74%). For parameters without significant interactions, repeated cytokinin applications increased leaf area, leaf area index, number of lateral shoots, plant dry weight, tuber growth rate, number of tubers per plant, and yield per plant compared with a single application. Three cytokinin applications produced the highest number of tubers per plant (15.15), whereas two applications produced the highest net assimilation rate and percentage of stolons forming tubers. Yield per plant did not differ significantly between two and three cytokinin applications. Three prohexadione-Ca applications reduced plant height and produced the highest net assimilation rate and relative growth rate, whereas two applications, at 49 and 56 days after planting, produced the highest plant dry weight, percentage of stolons forming tubers, number of tubers per plant (12.96), and yield per plant (77.91 g). These findings demonstrate that the most suitable application frequency depends on the targeted parameter in G_0 seed potato production under medium-altitude conditions.

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6. Conflict of Interest Declaration

The authors declare that there are no conflicts of interest related to the publication of this article. The authors confirm that this manuscript is original and free from plagiarism.

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C : **C**onceptualization
M : **M**ethodology
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8. Generative AI Statement

During the preparation of this manuscript, the authors used Grammarly and ChatGPT (OpenAI) to assist with English grammar correction, language refinement, paraphrasing, and improvement of the clarity and readability of the manuscript. All AI-generated suggestions were critically reviewed, edited, and validated by the authors to ensure accuracy, originality, and scientific integrity. Generative AI was used solely as a supportive tool and was not involved in generating original experimental data or independently conducting statistical analyses or interpreting research findings. The authors take full responsibility for the accuracy, integrity, and final content of the manuscript. Generative AI tools are not credited with authorship.

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About Author(s)

Sahrul Ramdhani is a master's student in the Master of Agronomy Program, Faculty of Agriculture, Universitas Padjadjaran, Sumedang, West Java, Indonesia, where his research interests include plant ecophysiology, potato cultivation, plant growth regulators, and seed potato production. ORCID iD: 0009-0009-2021-9775.

Dr. Rahmat Budiarto is an Assoc. Professor in the Department of Agronomy, Faculty of Agriculture, at Universitas Padjadjaran in Sumedang, West Java, Indonesia, specializing in production of tropical horticultural crops, plant secondary metabolites, and horticultural stress physiology. ORCID iD: 0000-0002-0479-2944.

Dr. Arya Widyawan is a researcher affiliated with King Saud University, particularly Department of Plant Protection, College of Food and Agricultural Sciences in Riyadh, Saudi Arabia. His specializing in plant-microbe interactions. ORCID iD: 0000-0003-2208-3794.

Dr. Supatida Abdullakasim is an Assoc. Professor in the Department of Horticulture, Faculty of Agriculture at Kamphaeng Saen, Kasetsart University, Thailand, specializing in horticultural crop physiology, controlled-environment agriculture (such as LED lighting for microgreens and herbs), and ornamental crop production. ORCID iD: 0000-0001-8258-6014.

Prof. Dr. Jajang Sauman Hamdani is a Full Professor in the Department of Agronomy, Faculty of Agriculture, Universitas Padjadjaran in Sumedang, West Java, Indonesia, specializing in horticultural production, especially potato cultivation. ORCID iD: 0000-0001-7861-1301.