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Optimizing L-DOPA production in velvet bean (*Mucuna pruriens*) through photoperiod and growth regulator manipulation

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ABSTRACT

Purpose: Due to the short-day nature of the velvet bean, which triggers flowering in the autumn with decreasing day length, its production in temperate and high-latitude regions under greenhouse conditions requires modifications in its flowering and fruiting habits. Therefore, this study aimed to optimize L-DOPA production by investigating photoperiod changes and hormonal regulation to encourage flowering and fruiting under greenhouse conditions**. Research Method:** Treatments included photoperiod at two levels (13-hour darkness and natural day length) as the first factor and growth regulators at seven levels (50 and 100 mg of gibberellin, 20 and 50 mg of paclobutrazol, 50 and 100 mg of cytokinin, and a control treatment) as the second factor. **Findings:** the effects of photoperiod, growth regulators, and their interaction were significant for all traits except for internode length. The natural light treatment resulted in a 3% delay in flowering compared to the 13-hour dark treatment, whereas the 13-hour dark treatment exhibited higher fruit weight, seed yield, and L-DOPA content (18%) compared to the natural light. Moreover, the application of 50 mg paclobutrazol reduced the days to flowering by 55 days compared to the control. On the other hand, the 50 mg paclobutrazol treatment showed significant increases in fruit weight (59%), seed yield (65%), and L-DOPA content (31%) compared to the control. **Research limitations:** No limitations were found. **Originality/Value:** Overall, extending the dark period improved velvet beans' yield and yield components. Furthermore, paclobutrazol enhanced yield more effectively than gibberellin and cytokinin. Based on the experiment, the best treatment for achieving maximum quantitative yield and L-DOPA content was 13-hour darkness combined with 50 mg of paclobutrazol.

INTRODUCTION

Medicinal plants play a pivotal role in the development of new drugs and the treatment of numerous diseases due to their valuable secondary metabolites, such as alkaloids, flavonoids, and terpenoids (Araghi et al., 2019; Behdad et al., 2020). Growth and secondary metabolites of medicinal plants are affected by several factors including genetic variability (Araghi et al., 2019; Bi et al., 2021; Duta-Cornescu et al., 2023), environmental stress (Behdad et al., 2021; Shahrajabian et al., 2023; Zarei et al., 2020), fertilizers (Heidari et al., 2014; Peng & Ng, 2022), agricultural practices during growth and after harvesting (Addo et al., 2021; Ebadi et al., 2017).

Given the emergence of drug resistance, the rise in chronic diseases, and the demand for cost-effective and sustainable therapies, humanity continues to explore and investigate new medicinal plant species to extract innovative compounds with high therapeutic potential. *Mucuna pruriens*, commonly known as velvet bean, is a tropical legume renowned for its rich nutritional and medicinal properties (Chen et al., 2023; Deli et al., 2020; Ritonga et al., 2023). Quantitatively, the plant is distinguished by its high L-DOPA content, a precursor to dopamine, constituting 3-7% of the seed's dry weight (Deli et al., 2020). Additionally, it contains significant amounts of protein (20-30%), carbohydrates, lipids, and essential minerals such as calcium, phosphorus, and iron (Ezegbe et al., 2023). Qualitatively, velvet bean exhibits diverse pharmacological activities, including antioxidant, anti-inflammatory, neuroprotective, and antidepressant effects (Fadilaturahmah et al., 2023). Its seeds are used in traditional medicine for treating conditions like Parkinson's disease, infertility, and snake bites (Lampariello et al., 2012). The plant's therapeutic efficacy is attributed to its bioactive compounds, including alkaloids, flavonoids, and saponins (Lampariello et al., 2012). Other notable characteristics of the velvet bean include its adaptability to various climatic conditions and its ability to grow in diverse soils, making it a versatile crop for agricultural and medicinal applications (Heuzé et al., 2015).

The velvet bean is a short-day plant that naturally enters the reproductive phase and flowers during the autumn season. For the sustainable production of this plant in temperate and high latitudes, particularly under greenhouse conditions, it is essential to modify its flowering pattern through precise photoperiod regulation and modulation of the hormones involved in flowering induction. On the other hand, growth regulators such as paclobutrazol, cytokinins, and gibberellins play crucial roles in modulating plant growth traits and yield components. Paclobutrazol, a triazole compound, primarily acts as a gibberellin biosynthesis inhibitor, reducing internodal elongation and overall plant height. This characteristic results in more compact and robust plants, which are beneficial for ornamental and crop plants grown in high-density environments (Desta & Amare, 2021). Furthermore, paclobutrazol enhances root growth, improves drought resistance, and increases chlorophyll accumulation, thereby boosting photosynthetic efficiency and stress tolerance (Tesfahun, 2018). Cytokinins, another class of plant growth regulators, are essential for promoting cell division and differentiation. They enhance shoot proliferation, leaf size, and delay senescence by maintaining chlorophyll content (Le Bris, 2017). Cytokinins also play pivotal roles in nutrient mobilization and lateral branch and bud formation, contributing to improved plant architecture and vigor (Wu et al., 2021). Their ability to delay leaf senescence while enhancing nutrient uptake can lead to higher crop yields and quality, particularly in fruits and vegetables (Jain et al., 2023). On the contrary, gibberellins are vital for various growth processes, including seed germination, stem elongation, and flowering. Gibberellins stimulate cell growth and division, resulting in taller plants with elongated internodes. They also break seed dormancy and aid in nutrient mobilization during germination, ensuring robust seedling growth. Additionally, gibberellins are critical for fruit development and growth, affecting fruit size and quality (Castro-Camba et al., 2022) .

Photoperiod, or day length, profoundly influences plant growth characteristics, yield, and its components. Photoperiod regulates key growth stages, including germination, vegetative growth, flowering, and fruiting (Yamamoto et al., 2008).Adequate day length increases photosynthesis, leading to robust vegetative growth and higher biomass accumulation (Chen et al., 2018). For instance, long-day conditions can accelerate stem growth and leaf expansion, while short-day conditions may hasten flowering and fruiting in short-day plants. This synchronization ensures optimal plant growth according to specific photoperiodic requirements (Chen et al., 2023). Insufficient photoperiods can delay flowering, reduce fruiting, and decrease yield. Conversely, optimal photoperiods enhance stress tolerance, improve nutrient utilization, and ensure uniform maturation, crucial for consistent quality and yield (Qin et al., 2022). By understanding and manipulating photoperiods, agronomists can enhance plant performance and crop yield, ensuring better adaptability to environmental conditions (Rai, 2022).

Due to the short-day nature of the velvet bean (*Mucuna pruriens*), which triggers flowering in the autumn with decreasing day length, its production in temperate and high-latitude regions under greenhouse conditions requires modifications in its flowering and fruiting habits. Therefore, this study aimed to optimize L-DOPA production by investigating photoperiod changes and hormonal regulation to encourage flowering and fruiting under greenhouse conditions.

MATERIALS AND METHODS

To examine the impact of growth regulators and photoperiod on growth and yield characteristics of velvet beans, an experiment was conducted in 2022 in the research greenhouse of the Horticultural Department at Ferdowsi University of Mashhad. The greenhouse temperature was maintained between 18–28 °C, with a relative humidity ranging from 40% to 80%. In addition, the light intensity at the plant canopy level ranged from 500 to 2500 μmol m^{-2} s^{-1}.The experiment followed a factorial design in a completely randomized layout with five replicates. The treatments included photoperiod in two levels (13-hour darkness and natural day length) as the first factor and growth regulators at seven levels, including six hours of seed soaking and foliar application during the vegetative growth stage (50 and 100 mg GA3, 20 and 50 mg paclobutrazol, 50 and 100 mg cytokinin, and control with no regulator) as the second factor.

Before planting, seeds were soaked for six hours in different concentrations of GA3, paclobutrazol, cytokinin (Benzyl Amino Purine), and control without regulator). GA3 was sourced from Merck in Germany, while paclobutrazol was procured from Naturism in China. Additionally, the cytokinin known as Benzyl Amino Purine was obtained from Duchefa Biochemie in the Netherlands. The seeds were stirred every 15 minutes using a glass rod for aeration. They were subsequently treated with carbendazim fungicide at a concentration of 2 g/L and transplanted into seedling trays filled with a substrate mixture of cocopeat and peat moss in a 2:1 ratio) The mixture exhibited an EC of approximately 0.1 mS/cm, a final pH of around 6.0, and limited nutrient levels) on February 4, 2022.
The seedlings were transplanted to the main field on March 6, 2022, at a spacing of 60×60 cm.

Foliar application of plant growth regulators regulators was conducted in early May during the active growth phase of the plants. The treatments consisted of various concentrations: 50 and 100 mg L^{-1} of gibberellin, 20 and 50 mg L^{-1} of paclobutrazol, 50 and

100 mg L^{-1} of cytokinin, along with a control treatment (no growth regulator applied). All treatments were applied once in the afternoon using a handheld sprayer. The objective of the application was to accelerate growth and improve the physiological characteristics of the plants. Each treatment was administered with precision to individual plants, following specific guidelines regarding formulation and concentration.

A dark treatment was also applied for a period of one month, from May 22 to June 21. During this period, plants assigned to the dark treatment group were covered daily with a black cloth three hours prior to sunset. This protocol created a photoperiod of 11 hours of natural light and 13 hours of darkness. The treatment was intended to simulate altered photoperiod conditions and assess its effect on plant development.

Irrigation was conducted using a drip system twice daily for 10 minutes (morning and evening). All treatments received the same general fertilization regimen. Plants were supplied with a balanced NPK fertilizer (20-20-20) from Valagro, Italy, at a concentration of 2 g L^{-1}. In addition, a micronutrient fertilizer (Brexil Combi, Valagro, Italy) was applied at a concentration of 1 g L^{-1} during the 4–6 leaf stage. An amino acid-based biostimulant (Megafol, Valagro, Italy) was also applied once, at a concentration of 1 g L^{-1}, during the pre-flowering stage.

Days from sowing to flowering were recorded to determine the number of days to flowering. At the end of the growth season, traits such as internode length, number of internodes to flowering, fresh and dry pod weight, 100-seed weight, number of seeds per plant, fresh and dry seed weight, pod yield per plant, seed-to-pod ratio, and L-DOPA content were measured. For L-DOPA measurement, the method of Nour El-Dien was used (Nour El-Dien et al., 2005). Seeds were ground into a fine powder, and 5 g of each sample was weighed. Each sample was mixed with 100 mL of 0.2 N hydrochloric acid for 24 hours. The samples were filtered through filter paper using a Buchner funnel. Extracts were diluted to 5 mL with a buffer (sodium acetate and acetic acid, pH 5). Each sample was mixed with 20 µL of 0.1 M iodine solution. After 5-6 minutes, absorbance was measured using a spectrophotometer at 500 nm. L-DOPA content was calculated against the standard curve (Fig. 1).

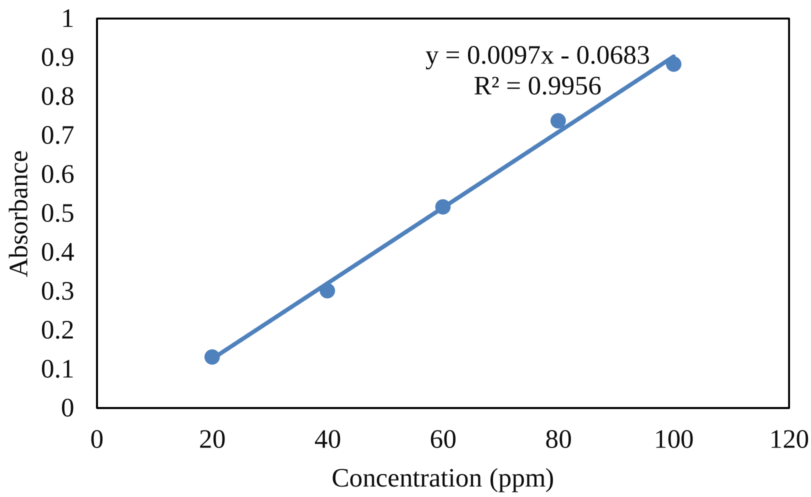

Fig. 1. L. DOPA concentration standard curve.

Statistical analysis

Data were analyzed using SAS 9.4 software. Mean comparisons were performed using Duncan's multiple range test at a 5% probability level. Figures were prepared using Excel.

RESULTS AND DISCUSSION

Days to flowering

The analysis of variance conducted on the examined traits revealed that the primary effects of photoperiod, growth regulators, and their interactions were statistically significant ($P \leq 0.01$) concerning the duration until flowering (Table 1). The findings demonstrated that plants subjected to natural light conditions took longer to reach flowering compared to those that experienced a 13-hour dark treatment. Furthermore, in both photoperiod scenarios, the application of 100 mg of cytokinin, along with the control treatment, resulted in an increased number of days required for flowering. Notably, a difference of five days in the flowering duration was recorded between the natural light and 13-hour dark treatments when considering the control condition. Furthermore, the greatest difference in days to flowering was recorded between the control treatment and the 50 mg paclobutrazol treatment, with 56 and 55 days under the 13-hour dark and natural light conditions, respectively (Fig. 2).

The phenological index of days to flowering is a critical parameter in plant biology, significantly influencing agricultural productivity and crop improvement. Previous studies have reported that short-day plants flower when day length decreases (Nagatani, 2017), consistent with the findings of this study. On the other hand, paclobutrazol, a plant growth regulator, has been shown to significantly influence flowering time. This compound inhibits gibberellin biosynthesis—a hormone essential for stem elongation, leaf expansion, and flowering (Novita, 2022). By reducing gibberellin levels, paclobutrazol can accelerate flowering (Novita, 2022). Sari et al. (2023) demonstrated that paclobutrazol increases early flowering by directing resources from vegetative to reproductive growth. The combined effects of photoperiod and paclobutrazol application are complex and species-specific. For instance, in long-day plants, paclobutrazol may counteract early flowering induced by extended daylight, resulting in a more balanced growth phase and improved plant structure. Additionally, paclobutrazol has been shown to accelerate flowering by increasing non-structural carbohydrates and redirecting photosynthetic products from leaves and stolons toward the crown (Desta & Amare, 2021). Moreover, paclobutrazol was reported to elevate phenolic compounds in terminal buds, altering the phloem-to-xylem ratio in stems. This shift restricts vegetative growth while enhancing flowering (Kumar et al., 2021).

Table 1. Analysis of variance for vegetative traits and yield components of velvet bean under the influence of photoperiod treatments and growth regulators.

Sources of Variation	d.f	(mean square)						
		Days to flowering	Number of internodes	Internode length	Pod fresh weight	Pod dry weight	100-seed weight	Number of seeds per plant
Photoperiod (A)	1	527**	46.4**	3.21ns	1320**	1893**	499**	5797**
Growth regulator(B)	6	5634**	13.4**	158**	3335**	2191**	1249**	52217**
A × B	6	264**	5.91**	46.9**	1300**	1043**	280**	25699**
Total error	56	7.45	0.693	1.61	121	96.5	3.66	648
C.V(%)		1.95	7.88	5.76	7.62	7.48	2.46	7.30

ns, * and ** are not significant, significant at five percent and one percent level, respectively.

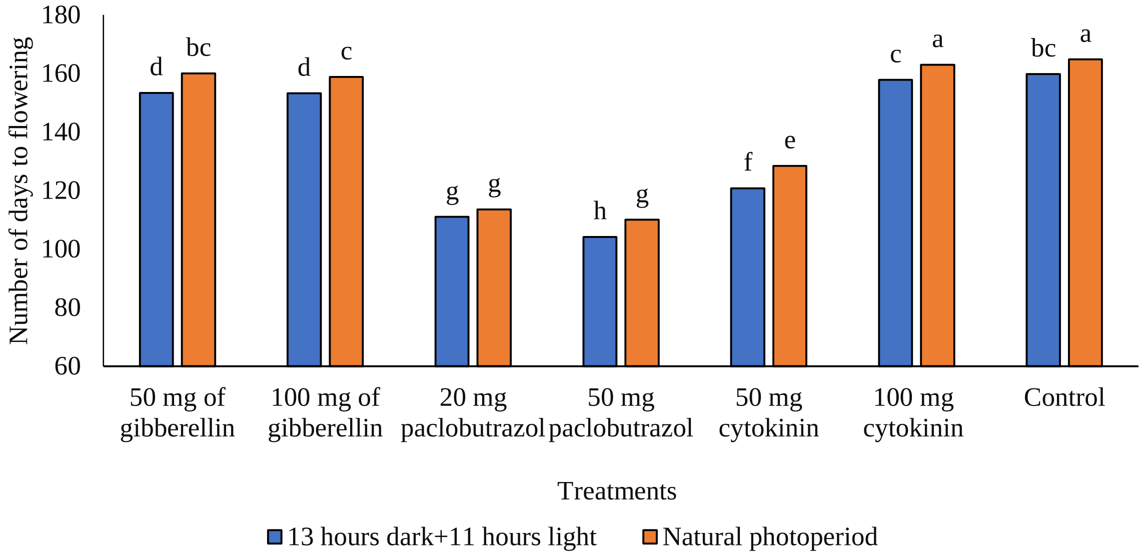

Fig. 2. Means comparison of the interaction between photoperiod and growth regulators on the number of days to flowering. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

Internode number and length

According to the results of the analysis of variance (Table 1), the simple effects of photoperiod and growth regulators and their interaction ($P \leq 0.01$) were significant for the number of internodes. Research indicates that plants cultivated under natural light conditions developed a greater number of nodules compared to those subjected to a regimen of 13 hours of darkness. Additionally, at both photoperiod treatments, the 100 mg cytokinin treatment resulted in a higher number of internodes. The number of internodes at the natural light in comparison to 13-hour darkness treatments for the 100 mg cytokinin was 10% more. Furthermore, the difference in the number of internodes between the highest (100 mg cytokinin) and the lowest (50 mg paclobutrazol) treatments was 26% under natural light and 57% under 13-hour darkness conditions, respectively (Fig. 3). The analysis of variance results presented in Table 1 showed that the main effect of growth regulators and the interaction between photoperiod and growth regulators were significant ($P \leq 0.01$) for internode length. According to the results mean comparison, the 13-hour darkness treatment had a longer internode length compared to the natural light treatment. Also, at both levels of light treatment, the 100 mg gibberellin treatment resulted in a greater internode length. The difference in internode length between the natural light and 13-hour darkness treatments for the 100 mg gibberellin treatment was 7%. Moreover, the difference in internode length between the greatest (100 mg gibberellin) and the lowest (20 mg paclobutrazol) treatments was 88% under 13-hour darkness and 65% under natural light conditions, respectively (Fig. 4).

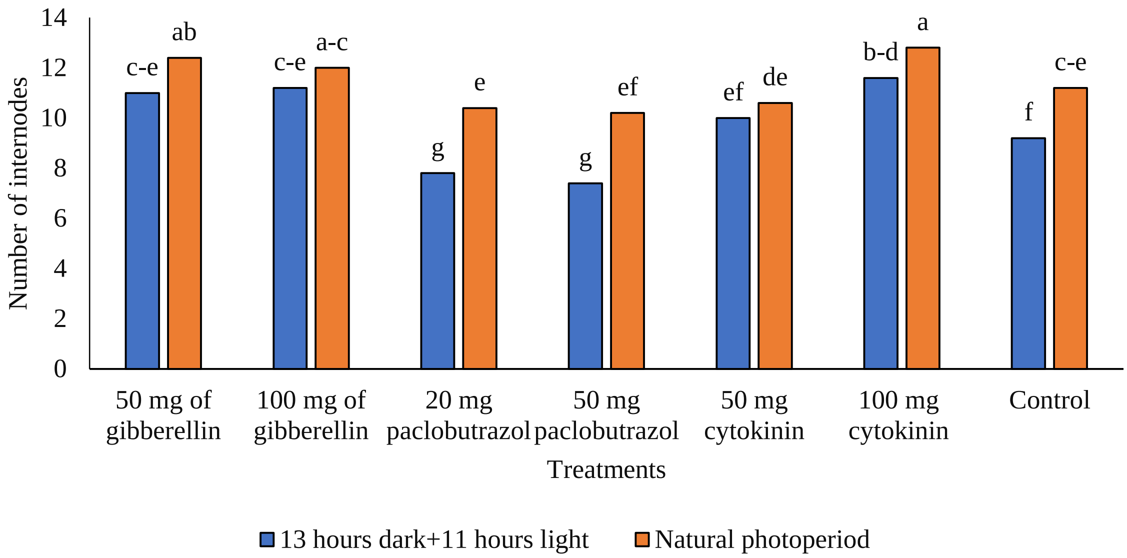

Fig. 3. Means comparison of the interaction between photoperiod and growth regulators on the number of internodes. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

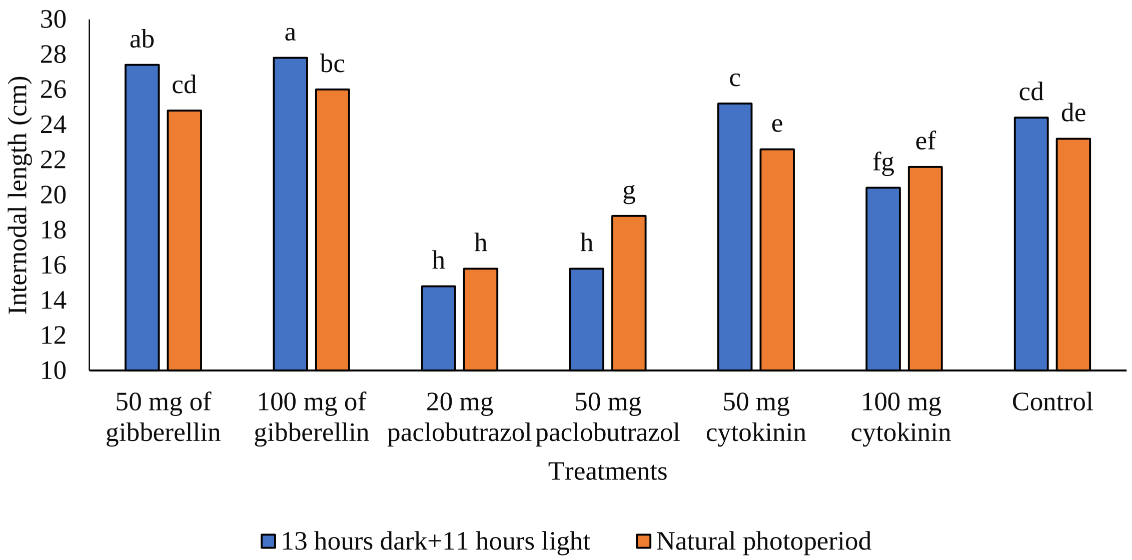

Fig. 4. Comparison of the means for the interaction between photoperiod and growth regulators on the internode length. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

This early flowering often results in fewer internodes in plants compared to those growing under long-day conditions. The limited number of internodes results from the rapid development of the reproductive organs, where the plant allocates more resources to flowering and seed production rather than vegetative growth (Hossain et al., 2017). In contrast, long-day conditions delay flowering in short-day plants, allowing for longer vegetative growth and potentially more internodes. Longer vegetative growth periods under long-day conditions can lead to increased branching and more internodes along the stem (Hossain et al., 2017). Under long-day conditions, due to the prolonged vegetative growth before flowering, internodes tend to elongate. In these conditions, there is more time for internodes to stretch, leading to greater internode spacing and potentially taller plants. On the other hand, cytokinin stimulates cell division, especially in meristematic tissues, resulting in the increased formation of new cells (Le Bris, 2017), which can contribute to the formation of more internodes along the plant stem. Conversely, gibberellin promotes cell elongation, contributing to longer internodes and increased plant height (Small & Degenhardt, 2018). Both cytokinin and gibberellin have been reported to play significant roles in promoting overall vegetative growth, including stem elongation and branch growth. This growth increase can result in more internodes and taller plants (Small & Degenhardt, 2018). These hormones are involved in various growth processes that affect plant morphology, including internode elongation and branching. Their activities are finely tuned to respond to environmental cues and internal signals, enabling plants to adjust their growth and development accordingly (Small & Degenhardt, 2018).

Fresh and dry pod weight

The results of the analysis of variance indicated that the main effects of photoperiod and growth regulators and their interaction were significant ($P \leq 0.01$) for the fresh and dry pod weight traits (Table 1). The results mean that the 13-hour darkness treatment had a higher fresh and dry pod weight than the natural light treatment. Additionally, at both levels of light treatment, the 50 mg paclobutrazol treatment resulted in a greater fresh and dry pod weight. The difference in pod weight between the 13-hour darkness and natural light treatments for the paclobutrazol treatment was 9% and 10%, respectively. Furthermore, the difference between the greatest (50 mg paclobutrazol) and the lowest fresh and dry pod weight for the control (without growth regulator) in 13-hour darkness and natural light conditions was 54% and 61% for fresh pod weight and 47% and 54% for dry pod weight, respectively (Fig. 5 and Fig. 6). In short-day plants such as velvet beans, the reduction in day length triggers flowering, which subsequently affects pod growth and their dry weight. Paclobutrazol, as a plant growth regulator, inhibits gibberellin biosynthesis, leading to reduced plant height and increased stem thickness (Desta & Amare, 2021). This regulation can redirect the plant's energy towards reproductive growth, thereby increasing pod formation and dry weight. Studies have shown that the use of paclobutrazol under optimal photoperiod conditions can lead to a significant increase in pod dry weight. This is because paclobutrazol increases carbohydrate allocation to the pods rather than promoting vegetative growth, thus improving both the quality and quantity of the yield (Flores-López et al., 2016). Similarly, in mung beans (*Vigna radiata*), the application of paclobutrazol under controlled photoperiod conditions resulted in a significant increase in dry pod weight and overall yield (Liu et al., 2022). Therefore, it can be stated that the interaction between the daily photoperiod and the application of paclobutrazol creates a synergistic effect, optimizing the reproductive growth efficiency and yield potential of these plants.

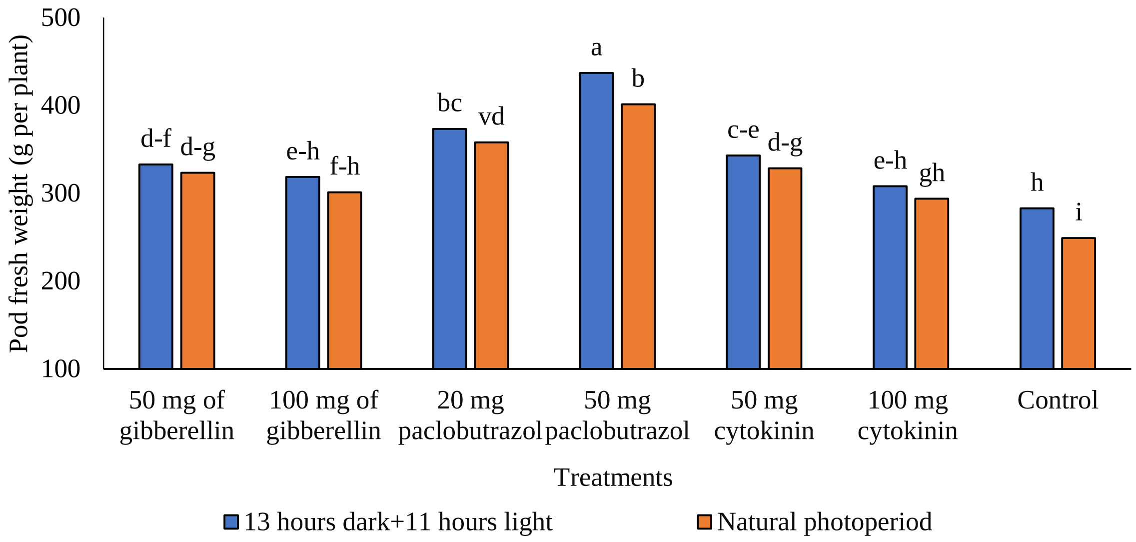

Fig. 5. Comparison of the means for the interaction between photoperiod and growth regulators on the pod fresh pod weight. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

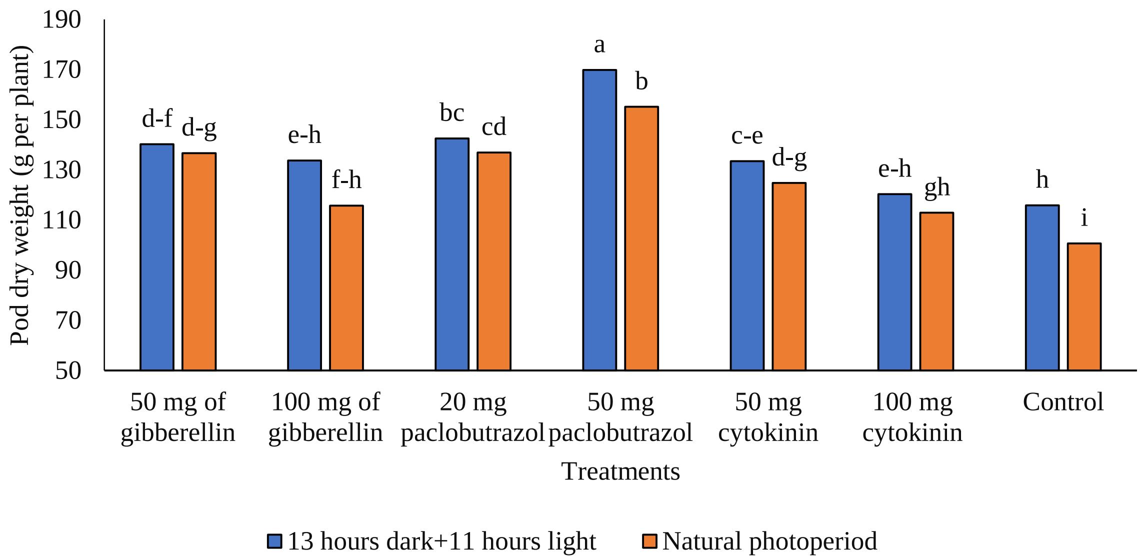

Fig. 6. Comparison of the means for the interaction between photoperiod and growth regulators on the pod dry pod weight. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

100 - Seed weight

Based on the results of the variance analysis of traits, the main effects of photoperiod and growth regulators, and their interaction, were significant ($P \leq 0.01$) for seed weight (Table 1). The results showed that the 13-hour dark treatment had a higher seed weight compared to the natural light treatment. Additionally, at both light treatment levels, the growth regulator treatment with 50 mg paclobutrazol resulted in higher seed weight. The 13-hour dark treatment with paclobutrazol resulted in a 4% increase in seed weight compared to the natural light treatment. Furthermore, the difference in the highest (50 mg paclobutrazol) and lowest seed weight for the control treatment without growth regulator under both the 13-hour dark and natural light conditions was 43% and 51%, respectively (Fig. 7). Seed weight, with increasing photoperiod, increased less primarily due to resource allocation and plant physiological responses. In longer day periods, plants often allocate more energy and resources to vegetative growth (such as leaves, stems, and roots) rather than reproductive growth (flowers and seeds). This is because longer days typically signal to the plant that the growing season is still progressing, with a reduced need for reproductive growth (Nord et al., 2011). Furthermore, in legumes, flowering is delayed with longer day length. This delay in flowering means that seed growth begins later in the season, leaving less time for seeds to fully develop and reach their maximum weight before the growing season ends (Springthorpe & Penfield, 2015). On the other hand, under extended photoperiod conditions, plants often produce more carbohydrates through photosynthesis. However, these carbohydrates are typically utilized to support continuous vegetative growth rather than being stored in seeds. As a result, less energy is directed toward seed filling, leading to lighter seeds (Springthorpe & Penfield, 2015). Moreover, paclobutrazol has an advantage in increasing seed weight due to its specific action focusing on growth regulation and resource allocation, compared to cytokinin and gibberellin. Paclobutrazol inhibits gibberellin biosynthesis, resulting in reduced vegetative growth and shorter, more compact plants (Taha & Srour, 2016). This shift in energy and nutrient allocation, away from excessive stem and leaf growth, facilitates more efficient allocation to reproductive structures such as seeds. As a result, paclobutrazol-treated plants typically have a higher seed weight. In contrast, cytokinin and gibberellin primarily enhance cell division and elongation, which can increase vegetative growth but may divert resources away from seed growth (Ritonga et al., 2023). While these hormones are beneficial in specific scenarios, they do not provide targeted control over resource allocation in the same way that paclobutrazol does, making paclobutrazol a more effective growth regulator for optimizing seed weight.

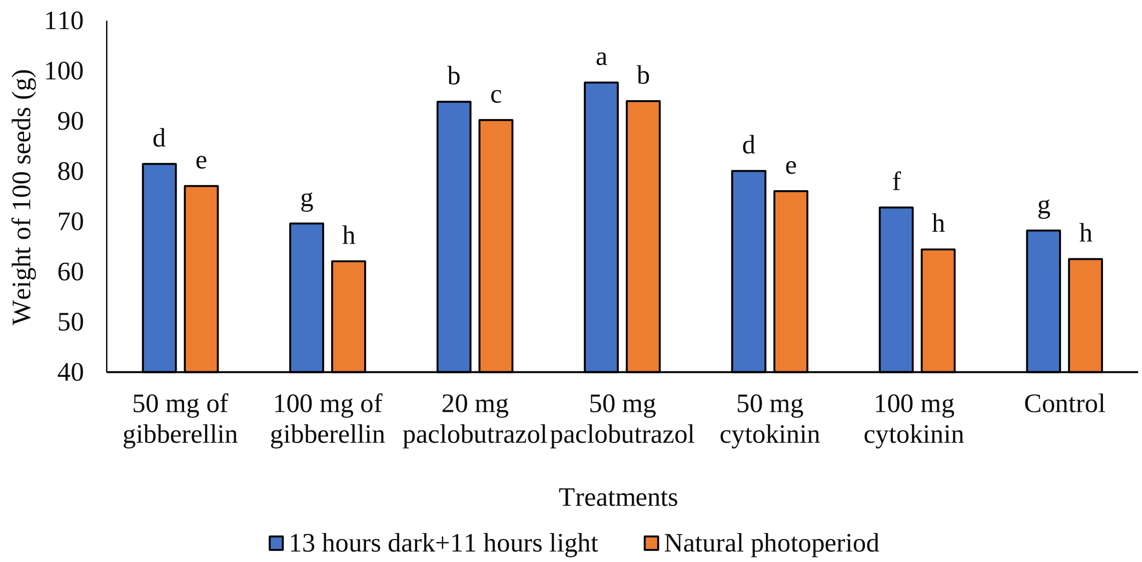

Fig. 7. Comparison of the means for the interaction between photoperiod and growth regulators on the 100-seed weight. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

Number of seeds per plant

Analysis of variance revealed that the main effects of photoperiod, growth regulators, and their interaction ($P \leq 0.01$) had a significant effect on the number of seeds per plant (Table 1). The results of the mean comparisons showed that, although the growth regulator treatments at two photoperiods levels (13 hours of darkness and natural light) did not show significant statistical differences, the 13-hour darkness treatment had a superior effect on the number of seeds per plant compared to the natural light treatment. Furthermore, at both photoperiod levels (13 hours of darkness and natural light), the highest number of seeds per plant was observed in the 50 mg paclobutrazol treatment, with differences of 146% and 170% over the control treatment, respectively (Fig. 8).

Short-day plants require a shorter light period to induce flowering. During the shorter days, these plants flower earlier and more synchronously, leading to a higher number of flowers, which can be converted into more seeds. Longer photoperiods may delay flowering, reduce the reproductive growth stage, and limit seed production potential (Qin et al., 2022) .Moreover, shorter photoperiods often lead to a shift in the allocation of plant resources from vegetative to reproductive growth. This means that the plant directs more nutrients and energy toward flower and seed growth rather than leaves and stems, which enhances seed production (Paltridge & Denholm, 1974). On the other hand, paclobutrazol inhibits gibberellin biosynthesis, resulting in shorter plants with reduced vegetative growth. This inhibition of vegetative growth directs the plant's nutrients and energy towards reproductive structures such as flowers and seeds rather than vegetative parts. The increased allocation to reproductive growth leads to an increase in the number of seeds per plant (Desta & Amare, 2021). Additionally, paclobutrazol promotes earlier and more synchronized flowering by reducing excessive vegetative growth, leading to a higher number of flowers, which can subsequently be converted into seeds. More flowers mean a greater potential for seed production (Desta & Amare, 2021).

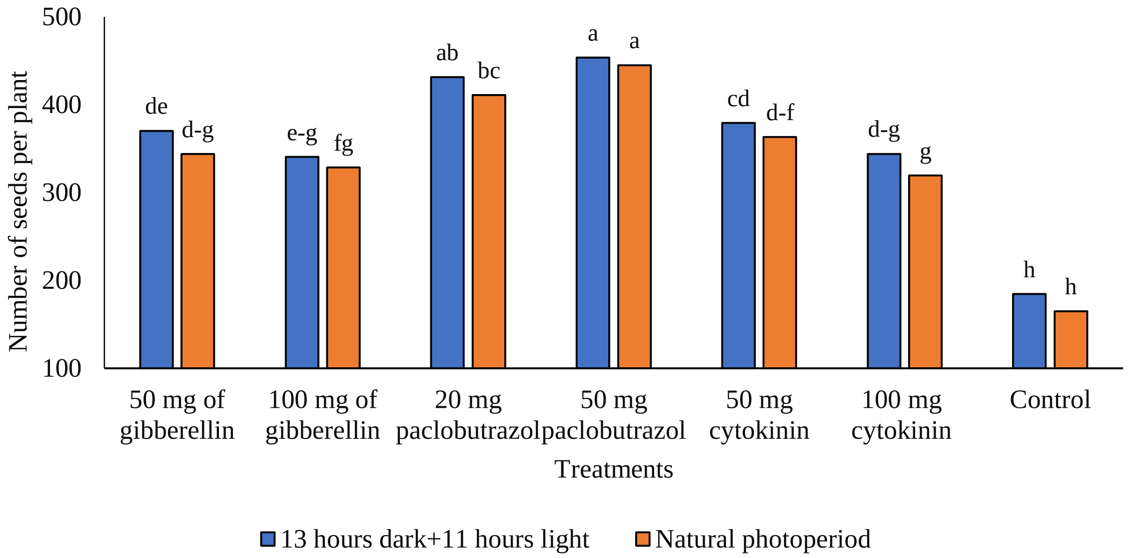

Fig. 8. Comparison of the means for the interaction between photoperiod and growth regulators on the number of seeds per plant. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

Fresh and dry seed weight

Analysis of variance results showed that the main effects of photoperiod ($P \leq 0.05$) and growth regulators, and their interaction ($P \leq 0.01$), were significant for the fresh seed weight trait, while the main effect of growth regulators and the interaction between photoperiod and growth regulator were significant ($P \leq 0.01$) for dry seed weight (Table 2). Mean comparisons indicated that the 13-hour darkness treatment had a higher fresh and dry seed weight compared to the natural light treatment. Additionally, at both levels of photoperiod treatment, the 50 mg paclobutrazol treatment had a higher fresh and dry seed weight. The difference in fresh and dry seed weight for the 13-hour darkness and natural light treatments under the paclobutrazol treatment was 2% higher, though this difference was not statistically significant. Moreover, the difference between the highest (50 mg paclobutrazol) and lowest fresh and dry seed weight for the control treatment without growth regulator under the 13-hour darkness and natural light conditions were 50% and 51% for fresh seed weight and 65% and 51% for dry seed weight, respectively (Fig. 9 and Fig. 10).

Longer days can lead to an uneven distribution of nutrients within the plant. With more resources directed toward vegetative growth, the growing seeds may receive fewer nutrients, which can limit their growth and weight (Tabatabaie et al., 2004).Moreover, long light hours can sometimes cause stress in certain plant species, affecting their overall growth and reproductive success. Stress conditions can lead to improper seed development and reduced seed weight (Resentini et al., 2023). Additionally, under shorter photoperiods, the reduced focus on vegetative growth means less internal competition for resources between vegetative and reproductive structures (Raihan et al., 2021). This balance supports higher reproductive yield, resulting in heavier seeds. On the other hand, it has been reported that the controlled and uniform growth induced by paclobutrazol application helps improve canopy management, enhances light penetration, and reduces competition between plants (Raihan et al., 2021). This can lead to better plant health and increased seed weight. In contrast, gibberellin and cytokinin primarily enhance vegetative growth. Gibberellin increases stem length and leaf expansion, which can lead to taller plants with more biomass but potentially fewer resources available for seed growth (Ritonga et al., 2023). Cytokinins promote cell division and branching, which can also result in more vegetative growth at the expense of reproductive yield (Zahir et al., 2001). While these hormones are beneficial for specific aspects of plant growth, they do not offer the targeted control over reproductive growth that paclobutrazol does.

Table 2. Analysis of variance for fruit and seed production and L-DOPA content of velvet bean, under the influence of photoperiod treatments and growth regulators.

Sources of Variation	d.f	(Mean square)					
		Fresh seed weight per plant	Dry seed weight per plant	Seed-to-pod ratio	Number of pods per plant	Fruit weight per plant	L-DOPA
Length of day (A)	1	4839*	357ns	0.180**	0.177ns	3863**	1.64 ns
Growth regulator (B)	6	67363**	13766**	0.298**	0.586*	35906**	5.03**
A × B	6	27507**	5604**	0.041**	0.571*	155*	1.50*
Total error	56	855	424	0.013	0.250	566	0.560
CV (%)		4.92	8.17	5.86	26.3	6.21	4.35

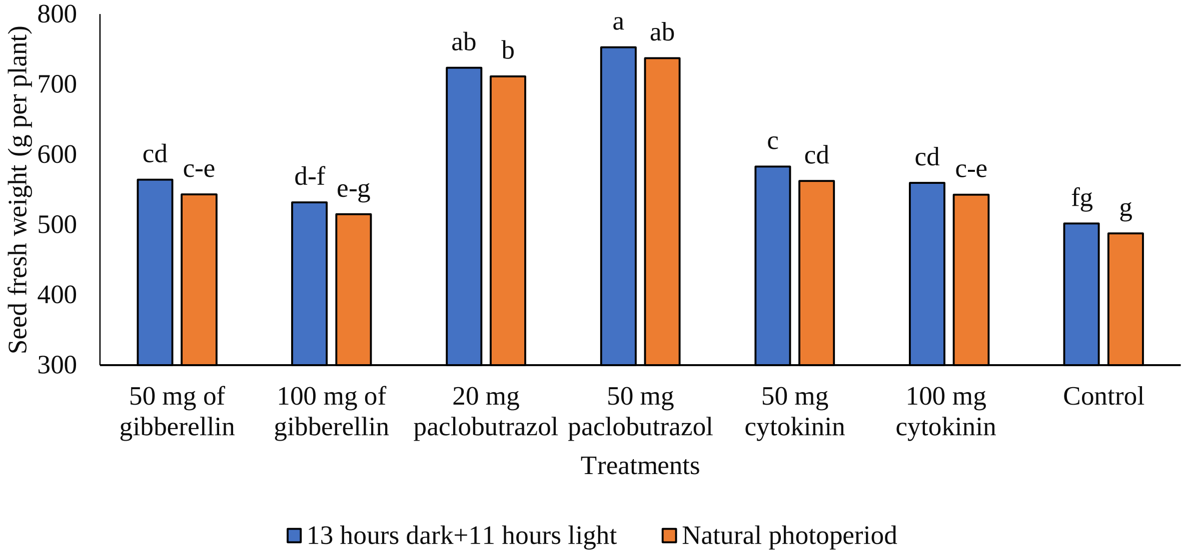

Fig. 9. Comparison of the means for the interaction between photoperiod and growth regulators on the fresh seed weight per plant. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

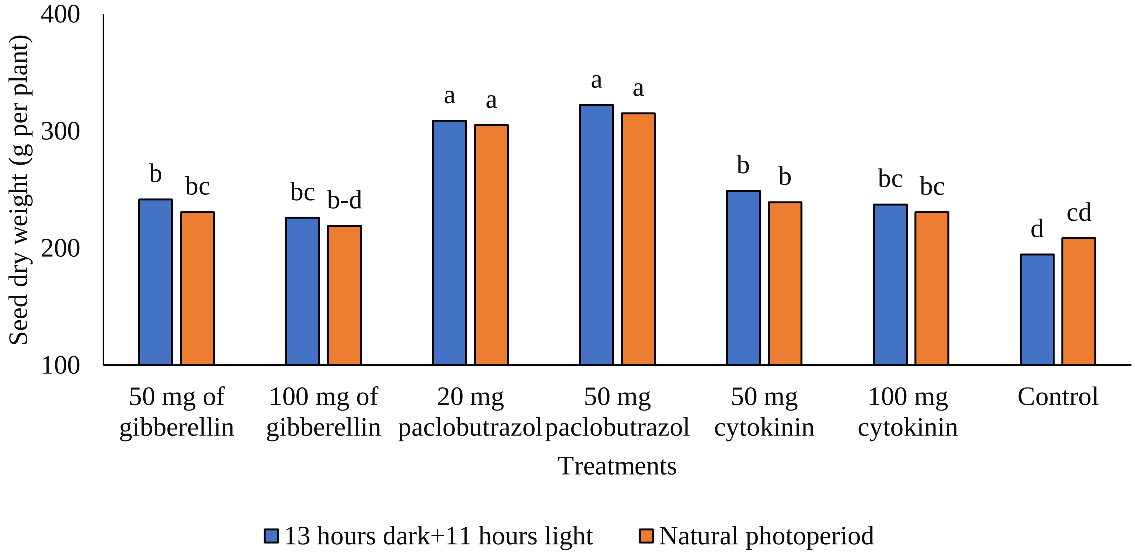

Fig. 10. Comparison of the means for the interaction between photoperiod and growth regulators on the dry seed weight per plant. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

Seed-to-pod ratio

The results of the analysis of variance (Table 2) showed that the main effects of photoperiod and growth regulators, as well as their interaction ($P \leq 0.01$), were significant for the seed-to-pod ratio. The results indicated that the natural light treatment had a higher seed-to-pod ratio compared to the 13-hour darkness treatment. Additionally, at both photoperiod treatment levels, the 20 mg paclobutrazol treatment exhibited a higher seed-to-pod ratio (3%). The difference in the seed-to-pod ratio between the natural light and 13-hour darkness treatments for the 20 mg paclobutrazol treatment was 3%. The seed-to-pod ratio was 32% higher for the 20 mg paclobutrazol treatment under natural light compared to the 50 mg gibberellin treatment, and 28% higher for the 20 mg paclobutrazol treatment under 13-hour darkness compared to the 100 mg gibberellin treatment (Fig. 11). During long photoperiods, plants experience extended vegetative growth before transitioning to the reproductive phase. This prolonged period allows for the accumulation of resources such as carbohydrates and nutrients.

Once the plant transitions to the reproductive phase, these resources are available for seed growth, leading to more seeds per pod (Raihan et al., 2021). Furthermore, longer day lengths may improve pollination and fertilization conditions. Longer photoperiods can promote better flower growth and increased pollinator activity, which could enhance the fertilization rate of flowers, leading to the development of more seeds in each pod (Kehrberger & Holzschuh, 2019). It has been reported that long days generally delay the transition to the reproductive stage in short-day plants. This delay ensures that when the plant starts forming flowers and pods, it has a strong vegetative structure and enough resources to support higher seed sets per pod (Osnato et al., 2022). On the other hand, paclobutrazol inhibits gibberellin biosynthesis, resulting in reduced stem elongation and overall vegetative growth. This inhibition helps redirect the plant's resources, such as nutrients and carbohydrates, from vegetative growth to reproductive growth, particularly toward seed growth (Novita, 2022). As a result, paclobutrazol-treated plants can produce more seeds per pod. Additionally, gibberellin and cytokinin primarily promote vegetative growth and cell division, which can result in taller plants with greater biomass but do not necessarily result in a higher seed-to-pod ratio. Gibberellin promotes stem elongation, which can lead to resource allocation towards vegetative structures rather than reproductive structures (Small & Degenhardt, 2018). Cytokinin promotes cell division and stem growth, which may divert resources from seed growth in the pods (Zürcher & Müller, 2016).

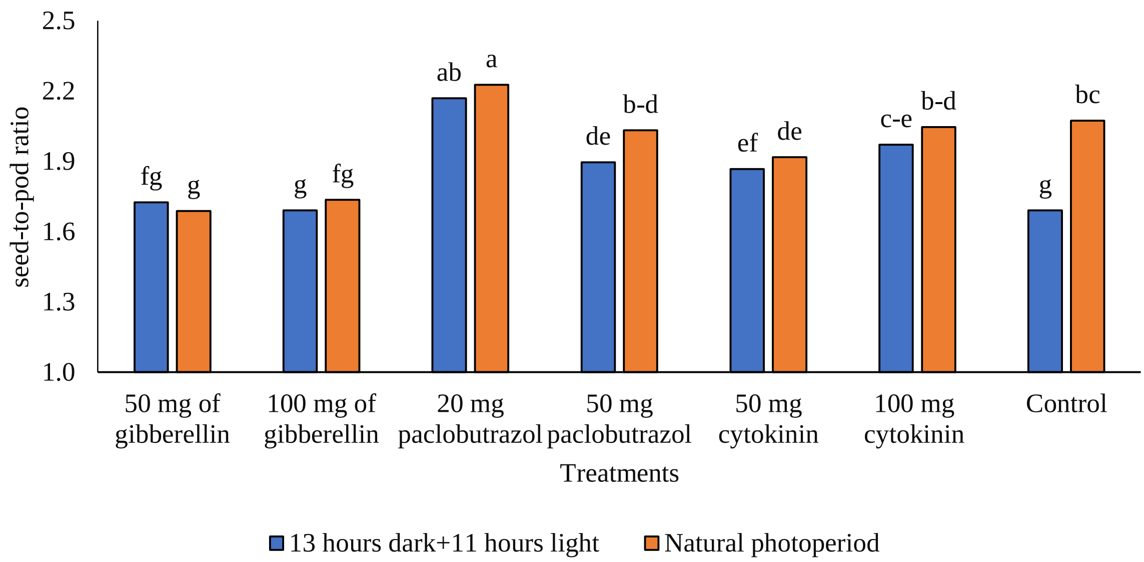

Fig. 11. Comparison of the means for the interaction between photoperiod and growth regulators on the seed-to-pod ratio. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

Fruit weight per plant

According to the results of the analysis of variance (Table 2), the main effects of photoperiod and growth regulators, as well as their interaction ($P \leq 0.01$), were significant for fruit weight per plant. The results showed that although the 13-hour darkness treatment did not significantly differ from the natural light treatment statistically, it had a higher fruit weight per plant. Additionally, at both light treatment levels, the 50 mg paclobutrazol treatment exhibited a higher fruit weight per plant. The difference in fruit weight per plant between the 13-hour darkness and natural light treatments for the paclobutrazol treatment was 5%. Furthermore, the difference between the highest (50 mg paclobutrazol) and lowest fruit weight per plant for the control treatment without growth regulators under 13-hour darkness and natural light was 59% and 52%, respectively (Fig. 12). Shorter days can lead to increased flowering and fruiting. This synchronization ensures that a higher percentage of flowers can be pollinated and simultaneously converted into seeds, thereby increasing the number of fruits and total seed count per plant (Qin et al., 2022). Many short-day plants are evolutionarily adapted to environments with shorter growing seasons. These plants have developed mechanisms to maximize reproductive success during the shorter days, leading to efficient seed production within the limited available time (Franks et al., 2007). It has also been reported that paclobutrazol treatment increases flowering and improves resource allocation toward seed growth, increasing the number of fruits and seeds per plant (Gerdakaneh et al., 2018). Gibberellin and cytokinin treatments, while enhancing overall plant growth, may not necessarily lead to a uniform increase in seed numbers due to their effects on increasing vegetative growth rather than reproductive growth. Therefore, paclobutrazol is more effective in increasing the number of fruits. Moreover, paclobutrazol enhances earlier and more synchronized flowering, which can lead to a better set of fruits and seeds in each pod. This synchronization ensures that a greater proportion of flowers are successfully fertilized and converted into fruits and seeds (Muniandi et al., 2018). Researchers have also stated that paclobutrazol, by controlling excessive vegetative growth, ensures that the plant's energy is effectively used for reproductive processes (Desta & Amare, 2021); (Tesfahun, 2018). This controlled growth results in a more balanced plant structure, focusing on producing more fruits.

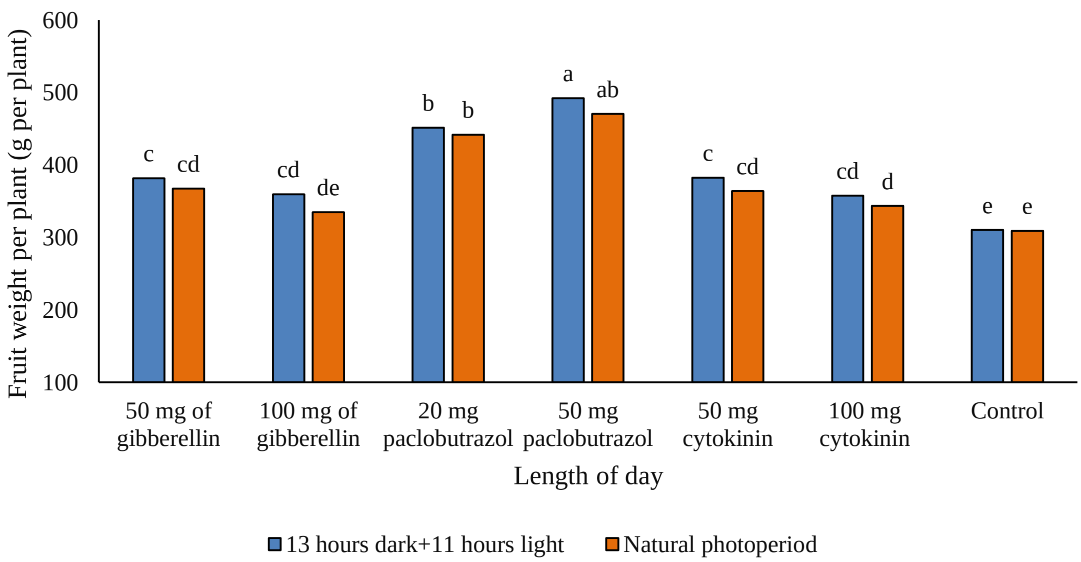

Fig. 12. Comparison of the means for the interaction between photoperiod and growth regulators on the fruit weight per plant. (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.).

L-DOPA content

According to the results of the analysis of variance (Table 2), the main effects of photoperiod, growth regulators, and the interaction between photoperiod and growth regulators ($P \leq 0.01$) were significant for L-DOPA content. The results indicated that the 13-hour darkness treatment had a higher L-DOPA content compared to the natural light treatment. Additionally, at both light treatment levels, the 50 mg paclobutrazol treatment exhibited higher L-DOPA content. The difference in L-DOPA content between the 13-hour darkness and natural light treatments for the paclobutrazol treatment was 18%. Furthermore, the difference between the highest (50 mg paclobutrazol) and lowest L-DOPA content for the control treatment without growth regulators under 13-hour darkness and natural light conditions was 31% and 40%, respectively (Fig. 13). Shorter days initiate the plant's flowering process and allocate resources from vegetative growth to reproductive pathways and secondary metabolites (Chrétien et al., 2022). This shift leads to increased L-DOPA synthesis as the plant prepares for reproductive growth. Moreover, shorter days often create mild stress conditions that can trigger the plant's defense mechanisms, boosting the production of secondary metabolites as a protective measure (Dufková et al., 2023). In contrast, long days promote vegetative growth and delay flowering, which leads to the dilution of resources as they are directed toward maintaining increased biomass rather than synthesizing secondary metabolites. Therefore, the physiological and metabolic adjustments caused by short-day conditions create an optimal environment for L-DOPA production, making short days superior for maximizing L-DOPA content in velvet beans compared to long days. Additionally, the superiority of paclobutrazol over gibberellin and cytokinin in increasing L-DOPA content in velvet beans can be attributed to its specific effects on plant physiology and secondary metabolite production. Paclobutrazol inhibits gibberellin biosynthesis, limiting excessive vegetative growth and directing the plant's metabolic resources toward secondary metabolite production, including L-DOPA. This growth regulation leads to smaller plants with higher metabolic efficiency, facilitating the synthesis and accumulation of more L-DOPA. Furthermore, paclobutrazol's effect on reducing vegetative growth minimizes competition for nutrients and energy, supporting L-DOPA biosynthesis (Desta & Amare, 2021). In contrast, gibberellin and cytokinin promote cell division and stem growth, which increases stem elongation and vegetative growth, potentially diluting secondary metabolite concentrations as resources are diverted to support increased biomass.

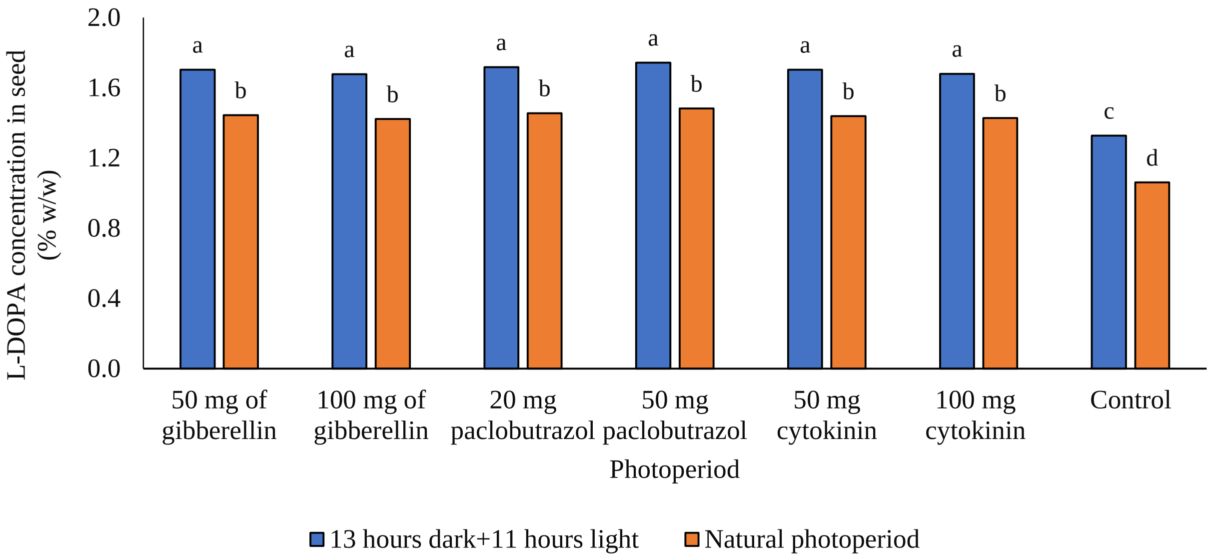

Fig. 13. Comparison of the means for the interaction between photoperiod and growth regulators on the L-DOPA Concentration in velvet bean seed (% w/w) . (Columns that share at least one common letter on top are not statistically different at the 5% level according to the Tukey test.)

CONCLUSION

Overall, the results of this experiment showed that increasing the duration of darkness increased the fresh fruit weight (437 gr/plant), dry fruit weight, hundred-seed weight, number of seeds per plant, fruit weight per plant, and L-DOPA content, while natural light led to an increase in growth characteristics such as the number of internodes. On the other hand, different levels of the growth regulator paclobutrazol were more effective than gibberellin and cytokinins in enhancing the yield of velvet bean plants. Based on the results of this experiment, the best treatment for achieving maximum quantitative yield and L-DOPA extraction was 13 hours of darkness combined with 50 mg paclobutrazol.

Conflict of interest

The authors declare that they have no conflict of interest.

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