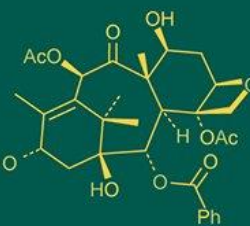
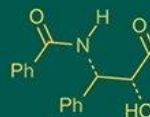
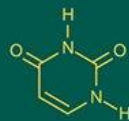


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Biological and hormonal regulation of potato microtuberization using jasmonic acid, benzylaminopurine and fungal filtrate

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Abstract

Potato (*Solanum tuberosum* L.) tuberization is a complex developmental process regulated by phytohormones and environmental cues. The present study evaluated the effects of jasmonic acid (JA), benzylaminopurine (BAP) and fungal filtrate on potato tuberization under *in vitro* conditions. Different concentrations of JA (0.5 ppm), BAP (1 and 2 ppm) and fungal filtrate (10 and 20 mL) were assessed for their influence on the percentage of tuberizing plants, tuber number per plant and tuber fresh weight. Among the treatments, 0.5 ppm JA significantly enhanced tuberization, producing 87% tuberizing plants, 6.1 tubers per plant and a tuber fresh weight of 14.8 g compared with the untreated control. BAP also promoted tuberization in a concentration-dependent manner, with 2 ppm BAP recording 91.6% tuberizing plants, 6.5 tubers per plant and 15.3 g tuber fresh weight. Application of fungal filtrate significantly improved all tuberization parameters, with 20 mL fungal filtrate increasing the percentage of tuberizing plants to 83.81% compared with 44.76% in the control, while also enhancing tuber number and tuber fresh weight. The stimulatory effect of the fungal filtrate is likely associated with the induction of endogenous jasmonic acid biosynthesis, potentially through the action of fungal metabolites such as theobroxide, which enhances lipoxygenase activity and jasmonate production. Overall, the findings demonstrate that JA, BAP and fungal filtrate effectively promote potato microtuberization, with fungal filtrate representing a promising biological elicitor for improving potato tuber production and productivity.

Keywords: Jasmonic acid, benzylaminopurine, fungal filtrate, theobroxide, tuberization

Introduction

Potato (*Solanum tuberosum* L.) is one of the important cool season rabi crop, originated in andean regions of South America esp. Peru. It has rich sources of starch, carbohydrates, proteins, fats and vitamins. Its required favorable environmental factors like low temperature, short days and plant hormones to induce tuberization in potato. One of the important factor is Phytohormones such as BAP (Benzyl adenine purine) and Jasmonic acid (JA) play an important role in the tuberization in potato.

Phytohormones such as cytokinins (CKs) are vital plant growth regulators that stimulate the development of potato tubers. BAP stands out as a crucial plant hormone for inducing micro-tuber formation in potato. Various concentrations of BAP have been employed and it has been suggested that, increasing BAP concentrations lead to higher numbers, weights and diameters of micro-tubers. Consequently, BAP is considered as a promising option for enhancing the quantity and quality of micro-tubers (Rahman *et al.*, 2015). More specifically BAP and kinetin significantly contribute to micro-tuberization in potato, influencing micro tuber number, size, weight and diameter (Borna *et al.*, 2019; Meenakshi, 2020). hence plant hormones play a significant role in potato tuberization (Bharath *et al.*, 2024).

The Jasmonic acid (Koda, 1997; Jackson, 1999) have been reported to regulate microtuber induction in potato. The combination of BAP levels with sucrose concentrations may contribute to improving micro-tuber size (Fufa and Diro, 2014). The Sembiring *et al.* (2020) reported the use of BAP and coconut water which can support the process of forming potato micro-tubers *in vitro*. Physiological results initially indicated that [16, 4, 13, 2, 11, 9, 5, 19],

low 6-benzyl amino purine (BAP) concentration advanced the tuberization beginning time and promoted tuber formation.

Cytokinins had detrimental effects on tuber growth and antagonized the action of jasmonates regardless of the maturity levels of the cultivars. However, they increased tuber dry matter, coinciding with a higher starch accumulation. The promoting effect of jasmonates on tuber dry matter and starch accumulation was evident mainly in early cultivars. Significant interactions between cytokinins and jasmonates were observed regarding the accumulation of reducing and total sugars in tubers. The findings indicate that, exogenous cytokinins counteract the effects of jasmonates and the intertwined actions of these two growth hormones vary with the maturity of the cultivar during potato tuber formation *in vitro* (Sarkar *et al.*, 2006).

Methyl jasmonate is a hormone known to modulate physiological events in plants such as encouraging tuber formation, functioning in vegetative development and fruit development. The results showed that, methyl jasmonate administration generally had no effect on vegetative growth (plant height, leaf number, and leaf area) of the potato plant. The methyl jasmonate application tends to decrease the number of tubers formed but increases the size and weight of the tubers. The treatment of methyl jasmonate does not affect the vegetative growth, height, leaf number and leaf area of potato plants (Rohmawati and Dewi, 2019).

The effects of jasmonic acid (JA) and methyl-jasmonate (MeJA) on potato tuberization were studied concerning cytokinins using single-node cuttings (SNCs) *in vitro*. While jasmonates promoted root growth, BA inhibited root growth and counteracted the stimulatory effects of jasmonates. BA also strongly inhibited stoloniferous shoot growth and had a more pronounced inhibitory effect when combined with jasmonates. Nevertheless, Jasmonates did not play a significant role in tuber induction in terms of tuber number and source-sink coordination (harvest index). Instead, their effects were countered in the presence of 22.0 μM BA in early cultivars. However, jasmonates did promote tuber growth after induction in early cultivars potentially due to their lower levels of endogenous gibberellins (Sarkar *et al.*, 2006).

Jasmonates (JAs) do not work independently but work as a part of a complex signaling network with other phytohormones (Yang *et al.*, 2019). Application of JAs seems to be promising during different steps of the micropropagation system for different species. JAs stimulate proliferation rate of shoots, roots, callus and induce micro-tubers and bulblets formation. The crosstalk between JAs and other phytohormones (mainly cytokinins, auxins and gibberellins) seems to be crucial for shoot proliferation, rooting and embryogenesis efficiency of different species. Particularly interaction linking JAs responses with gibberellins signaling pathway is a key factor determining explant growth and tuberization process. Knowledge about the mechanism of JA action in explants will provide useful information especially important for species with problematic propagation and micro-propagation system (Kamińska, 2021) [17, 18, 10].

JA has been found in leaves of several species. Its physiological role is associated with senescence. It is conceivable that, as a response to a photoperiodic regimen working as a biological clock, JA may be produced. Once available, JA would act as a chemical signal to trigger senescence-related processes like tuberization, which take

place after a sufficient vegetative development of the potato plant. Tuberization in both cases was associated with a decrease in rooting ability. Jasmonic acid also triggered a general state of induction throughout the stolon (Pelacho and Mingo-Castel, 1991).

The increase in LOX which is activated by low temperature results in large amounts of endogenous JA, TA and TAG which have a crucial role in potato tuber induction (Nam and Yoshihara, 2008). Theobroxide, isolated from the culture filtrate of the fungus *Lasiodiplodia theobromae* has been proposed as a natural tuber inducing compound in potato plants. Exogenously applied theobroxide strongly induced potato tuberization *in vitro* and *in vivo* under non-inductive photoperiod conditions (Yoshihara *et al.*, 2000) and stimulated the activity of LOX and endogenous levels of JA and TA (Gao *et al.*, 2003). Furthermore, theobroxide promoted the potato tuberization at low temperature which is suitable for tuber induction.

Effect of fungal extract on tuberization in potato A fungus *Lasiodiplodia theobromae* has been shown to synthesize a novel bio-organic compound known as Theobroxide, an epoxy cyclohexane compound has a role in stimulating potato tuber formation under non-inductive conditions. Like Jasmonic acid, theobroxide stimulates tuber induction through GA regulation (Yamashita *et al.*, 2016). In the present study, instead of pure theobroxide compound, the fungal extract of *Lasiodiplodia theobromae* was sprayed on to the *in vitro* grown potato plants planted on a mini-modular aeroponic chambers. The effect of fungal exudates was assessed by measuring the stolon formation as well as mini tuber induction and compared with control plants.

Theobroxide is an epoxy cyclohexene natural compound isolated from the fungus *Lasiodiplodia theobromae* and has a significantly inductive effect on potato tuber formation *in vitro* and *in vivo* condition. The influence of theobroxide on endogenous levels of JA and its analogue tuberonic acid (TA) as well as on lipoxygenase (LOX) activity in potato leaves was investigated. Results suggest that, the inductive effect of theobroxide on tuber formation is probably achieved by stimulating JA and TA synthesis (Gao *et al.*, 2003). When sprayed on potato leaves, theobroxide induces tubers even under non-inducing conditions (i.e., long days). These results will promote field tests of theobroxide which may enable the production of potato plants under long-day conditions (Arimoto *et al.*, 2005).

Theobroxide, a natural product, strongly stimulates the biosynthesis of jasmonic acid (JA) in *Pharbitis nil*. The effect of JA on the accumulations of these proteins was monitored simultaneously. The results show that, theobroxide treatment led to a high level accumulation of JA which is due to high accumulations of LOX, AOS and AOC proteins induced by theobroxide treatment both under short day (SD) and long day (LD) conditions (Kong *et al.*, 2005) [15, 14, 22, 7, 20, 7, 1, 12].

Material and methods

Planting material

The experiments were conducted at the Plant Tissue Culture Laboratory, Department of Crop Physiology, University of Agricultural Sciences, GKVK, Bangalore, India. The virus-free planting material of potato (*Solanum tuberosum* L.) cultivar, Kufri Jyothi (KJ) and Kufri Himalini (KH) was procured from the Central Potato Research Institute (CPRI),

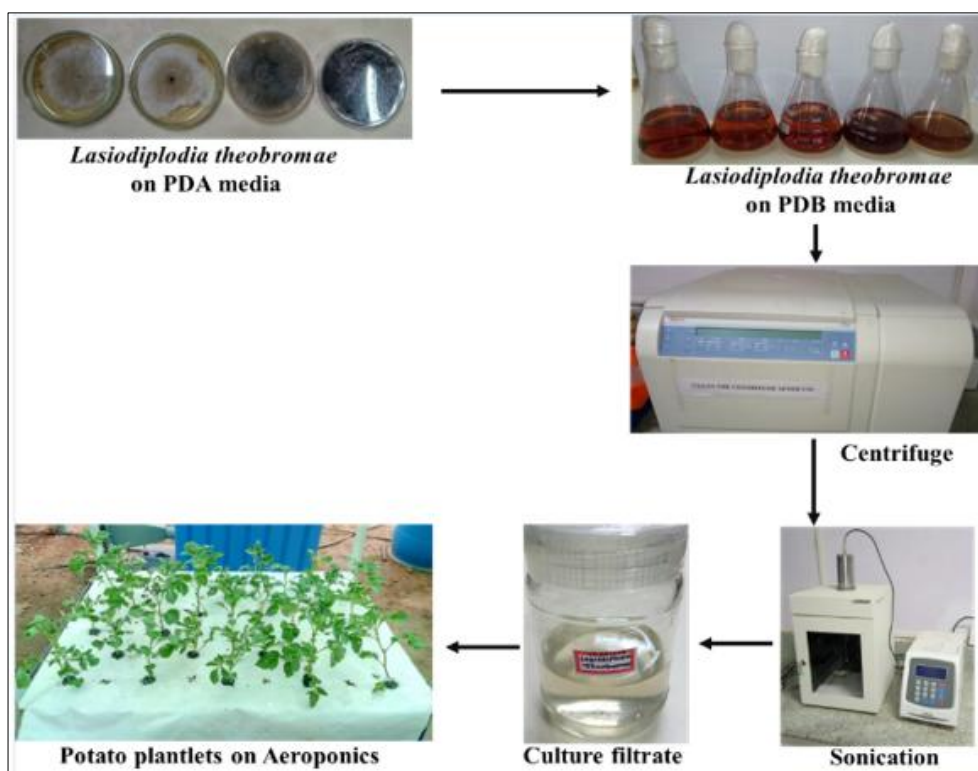
Shimla, India the College of Horticulture, Bengaluru campus, UHS, Bagalkot. for the experiments.

Effect of fungal extract on tuberization in potato

A fungus *Lasioidiplodia theobromae* has been shown to synthesize a novel bio-organic compound known as Theobroxide, an epoxy cyclohexane compound has a role in stimulating potato tuber formation under non-inductive conditions. Like Jasmonic acid, theobroxide stimulates tuber induction through GA regulation (Yamashita *et al.*, 2016). In the present study, instead of pure theobroxide compound, the fungal extract of *Lasioidiplodia theobromae* was sprayed on to the *in vitro* grown potato plants planted on a mini-modular aeroponic chambers. The effect of fungal exudates was assessed by measuring the stolon formation as well as mini tuber induction and compared with control plants.

Preparation of potato dextrose agar and potato dextrose broth for Fungi culture: The medium was prepared by suspending 39 grams of Potato Dextrose Agar or 24 grams of

Potato Dextrose Broth in 1 liter of purified distilled or deionized water ensuring thorough mixing. The mixture was heated with frequent agitation and it was boiled for 1 minute to completely dissolve the powder. Subsequently, the solution was autoclaved at 121°C for 15 minutes. For the medium in bottles, the contents of the bottles were melted in a water bath at 100°C leaving the cap partially removed until complete dissolution. Afterward, the cap was secured and the homogeneity of the dissolved medium was assessed by turning the bottle upside down, if necessary. The solution was cooled to 45-50 °C, mixed well to prevent foam formation and aseptically distributed into Petri dishes. Note: The agar medium's reaction to pH 3.5 was modified by cooling the base to 45-50°C, and an appropriate amount of sterile 10% tartaric acid was aseptically introduced to each liter of medium. Thorough mixing was ensured. Reheating of the medium was avoided. Alternatively, for fungal counts, bacterial growth was inhibited by adding 1 ml of 10% lactic acid to every 100 ml of sterilized medium at 50°C thereby acidifying the pH to approximately 3.5.



Flowchart 1: Effect of fungal filtrate on microtuberization in potato. The picture illustrates the steps followed to extract the fungal extract from *Lasioidiplodia theobromae* and sprayed onto the plants: (PDA: Potato Dextrose Agar; PDB: Potato Dextrose Broth)

First, potato dextrose agar (PDA) was prepared under aseptic conditions and it was allowed to solidify inside the laminar air flow (LAF). The fungus *Lasioidiplodia theobromae* was inoculated into the PDA and it was placed in a mechanical shaker for approximately two weeks to promote fungal growth. After *Lasioidiplodia theobromae* had been cultured in the potato dextrose agar, one loopful of the fungus was introduced into potato dextrose broth for robust fungal multiplication. Subsequently, the fungi broth filtrate and mycelium were collected for centrifugation. The mycelium was sonicated using a sonicator to release compounds and the fungi filtrate was then gathered (as depicted in Flowchart 1). The fungus, *Lasioidiplodia theobromae* had been harvested from the PDA media and inoculated into PDB media. Once the fungal culture attained the desired stage, it was harvested

by separating the mycelium from the liquid medium achieved through filtration. The filtration system was sterilized and the culture was filtered using a suitable filter such as a syringe filter or membrane filter to obtain a clear fungal filtrate. The fungal filtrate was then centrifuged at an appropriate speed (e.g., 4000 rpm) for a duration of 5 minutes to separate the liquid from any remaining solid components. The fungal filtrate was diluted with sterile water or a suitable buffer if necessary, often performed to bring the concentration within the linear range of the quantification method. The concentrated fungal filtrate was dissolved in distilled water and then diluted to 100 ppm with Tween-20. The diluted fungal filtrate was used for three treatments: a control with water spray and two others with 10 ml and 20 ml of fungal filtrate which were sprayed onto potato leaf samples and

stolon zones to assess the tuberization process in potato. The per cent tuberizing plants, number of tubers per plant and fresh weight of tubers were recorded.

To examine whether the fungal extract behaves similar to that of JA and Cytokinin, aeroponically grown plants were sprayed with JA and Cytokinin separately and the tuberizing response was recorded.

Statistical Analysis

The data on per cent tuberizing plants, tuber number per plant, tuber size and tuber fresh weight were collected during harvest. Further, all the collected data were analyzed by analysis of variance and the means were compared according to DMRT (Duncan's Multiple Range Test) and the mean separation was done at 5 and 1 per cent level of significance.

Results and discussion

The influence of Jasmonic acid and fungal extract on tuberization in potato

Jasmonic acid (JA), a plant hormone renowned for its multifaceted roles in stress responses, defense mechanisms and developmental processes has recently taken center stage

in the study of tuberization (Nam and Yoshihara, 2008; Gao *et al.*, 2003) [14, 7]. This phytohormone involvement in signaling cascades regulating diverse physiological responses suggests its potential influence on the intricate molecular mechanisms governing the transition from vegetative to reproductive growth in potato.

In the intricate of potato tuberization, the interplay of signaling molecules orchestrates a harmonious transition from vegetative growth to the formation of underground storage structures. The application of jasmonic acid (JA) at a concentration of 0.5 ppm demonstrated a significant positive impact on tuberization in potato plants. The percentage of tuberizing plants was notably higher at 0.5 ppm of JA (87%) compared to control and 1 ppm of benzyl amino purine (BAP), 10 ml and 20 ml of fungal filtrate (Figure 1). These findings suggest that, the application of 0.5 ppm of JA has a pronounced stimulatory effect on potato tuberization outperforming other tested treatments including the commonly used plant growth regulator, BAP and fungal filtrates. The observed increase in tuberization parameters highlights the potential of JA as a valuable tool in enhancing potato yield and tuber quality.

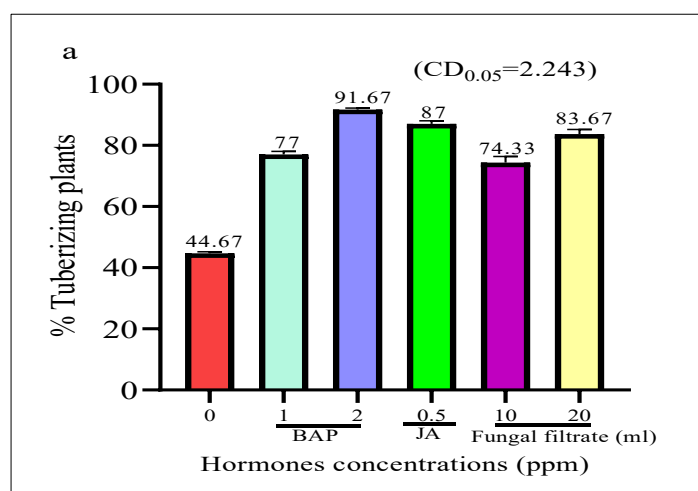


Fig 1: Effect of BAP, JA and fungal filtrate on micro-tuberization response in potato. (a) Percent tuberizing plants

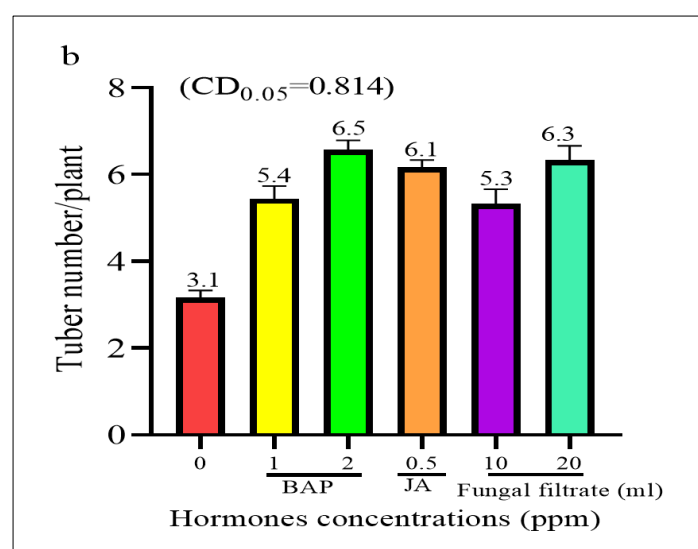


Fig 2: Effect of BAP, JA and fungal filtrate on micro-tuberization response in potato. (b) Tuber number per plant

Jasmonic acid production through some other means also trigger tuber production in potato. Accordingly, Theobroxide, a natural substance derived from a specific fungal, exhibits a

remarkable capability to stimulate the biosynthesis of JA, a phytohormone renowned for its multifaceted roles in plant development and stress responses. JA synthesized from α -

linolenic acid in plastids and peroxisome undergoes β -oxidation leading to production of TA (Tuberic acid) and TAG (Tuberic acid glycoside) resulting in tuberization in potato (Nam and Yoshihara, 2008). Theobroxide, an epoxy cyclohexane compound isolated from fungus *Lasiodiplodia theobromae* (Flowchart 1), increased lipoxygenase activity leading to enhance JA and TAG compounds which ultimately enhance tuberization (Wasternack and Strnad, 2018) [14, 18].

The influence of benzyl amino-purine (BAP) and fungal extract on tuberization in potato

The application of 1 ppm and 2 ppm concentrations of BAP led to a substantial increase in the percentage of tuberizing plants, reaching 77% and 91.6%, respectively compared to the control treatment's 44.67%. This outcome highlights a positive correlation between BAP concentration and the induction of tuberization in potato plants. Intriguingly, the 0.5 ppm concentration of JA unexpectedly demonstrated a significant enhancement in the percentage of tuberizing plants (87%) compared to the control treatment, suggesting a potential pivotal role of lower JA concentrations in promoting tuberization in potato. Equally noteworthy has been, both 10 ml and 20 ml of fungal extract exhibited a substantial increase in the percentage of tuberizing plants (74.33 and 83.67% respectively) compared to the control treatment (44.67%), signifying the positive impact of fungal extract on

tuberization in potato plants (Figure 1). This study not only reinforces previous findings on BAP's role in promoting tuberization but also unveils Theobroxide's potential as a less-explored plant growth regulator that could play a crucial role in enhancing tuberization. Further investigations into the mechanisms through which fungal extract induces tuberization are warranted as its efficacy may pave the way for innovative approaches in potato crop management (Bharath *et al.*, 2024; Gao *et al.*, 2005) [2, 6].

The investigation unveiled notable variations in the number of tubers per plant compared to the control treatment. Applying concentrations of 1 ppm and 2 ppm of BAP led to a significant increase in tuber numbers per plant (5.4 and 6.5, respectively) compared to the control treatment's (3.1). This implies a positive correlation between BAP concentration and the augmentation of tuberization in potato plants. Interestingly, the use of 0.5 ppm JA resulted in a considerably higher tuber number per plant (6.1) compared to the control treatment (3.1). Moreover, the application of 10 ml and 20 ml of fungal extract demonstrated a substantial increase in the number of tubers per plant (5.3 and 6.3 respectively) compared to the control treatment (3.1). These findings suggest a dose-dependent effect of fungal extract on tuberization in potato plants with higher concentrations leading to more pronounced tuber development (Figure 2).

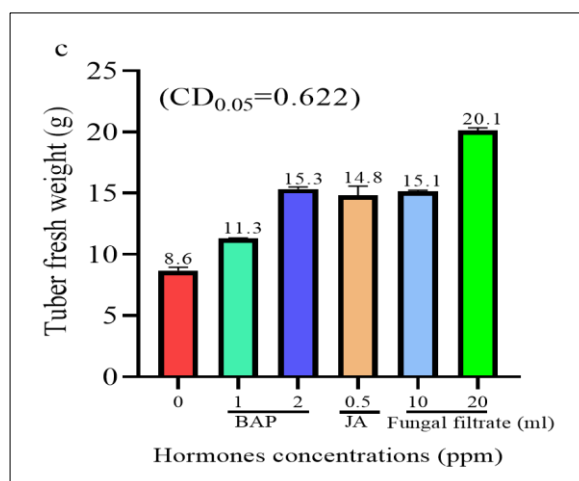


Fig 3: Effect of BAP, JA and fungal filtrate on micro-tuberization response in potato. (c) Tuber fresh weight (mg)

Examining tuber fresh weight, both 1 ppm and 2 ppm concentrations of BAP exhibited significantly higher weights at 11.3 g and 15.3 g, respectively compared to the control treatment (8.6 g). This indicates a positive influence of BAP on tuberization in potato at these respective concentrations. The tuber fresh weight at 0.5 ppm concentration of JA was notably higher at 14.8 g than the control treatment (8.6 g), suggesting a positive effect on tuber development in potato. Similarly, both 10 ml and 20 ml volumes of fungal extract showed a significant increase in tuber fresh weight at 15.13g and 20.11g, respectively compared to the control treatment (8.68g). This implies that, the application of fungal extract at these volumes positively promoted tuberization in potato (Figure 3; Plate 1).

Notably, Theobroxide, a natural compound from the fungus *Lasiodiplodia theobromae*, exhibits a significant inductive effect on potato tuber formation in both *in vitro* and *in vivo* conditions. These results suggest that, Theobroxide's inductive impact on tuber formation is likely achieved

through the stimulation of JA and TA synthesis as well as lipoxygenase (LOX) activity (Gao *et al.*, 2003) [7].

Effect of fungal filtrate on micro-tuberization response in potato

Application of 20 mL of fungal filtrate significantly increased the percentage of tuberizing potato plants, reaching 83.81%, compared with 44.76% in the untreated control (Figure 4a). This substantial improvement indicates that, the fungal filtrate effectively promotes tuberization in potato plants. The enhanced tuberization may be associated with an increase in endogenous jasmonic acid (JA) levels, as jasmonic acid is a well-established signaling molecule involved in the regulation of tuber initiation and development. Therefore, it is likely that the fungal filtrate stimulates JA biosynthesis or signaling pathways, thereby inducing and enhancing the tuberization process. Microtuber production was inhibited in the presence of GA3 (Hossain *et al.*, 2017) [8]. The maximum number of microtubers was observed when the explants were

planted vertically and were grown in two- phase medium which did not contain GA3 and had 10 ng/L JA. It was determined that, two-phase medium with 0.2 mg/L JA but

without GA3 was the most favourable medium for tuber growth (for both height and width).

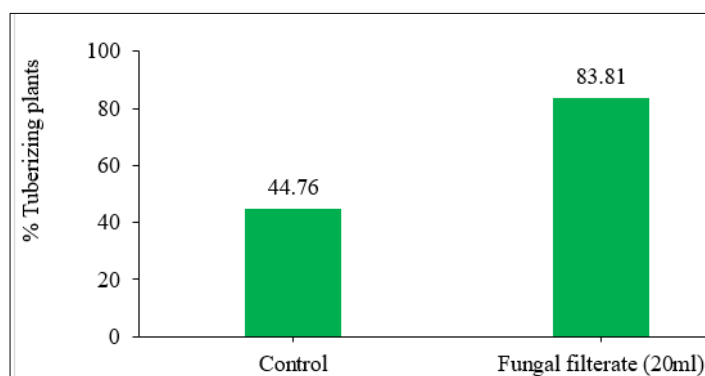


Fig 4a: Effect of fungal filtrate on micro-tuberization response in potato. a) Per cent tuberizing plants

In addition to increasing the percentage of tuberizing plants, the fungal filtrate also had a significant positive effect on tuber production. Plants treated with the fungal filtrate produced a significantly higher number of tubers per plant than the untreated control (Figure 4b). This finding suggests that the fungal filtrate not only promotes tuber initiation but also enhances the overall reproductive efficiency of potato plants.

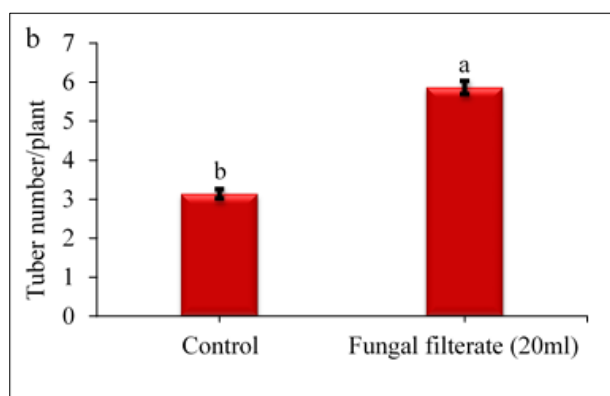


Fig 4b: Effect of fungal filtrate on micro-tuberization response in potato. b) Tuber number per plant

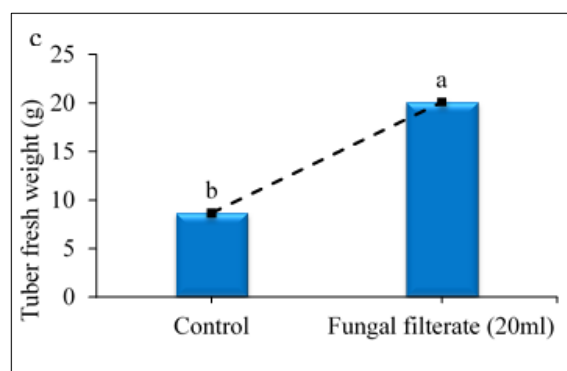


Fig 4c: Effect of fungal filtrate on micro-tuberization response in potato. c) Tuber fresh weight



Plate 1: Effect of different concentrations of Phytohormones on tuberization in potato (a) microtuber

Furthermore, treatment with the fungal filtrate resulted in a significant increase in the fresh weight of tubers compared with the control treatment (Figure 4c; Plate 2). The increase in tuber fresh weight indicates improved tuber growth and biomass accumulation, which may be attributed to enhanced nutrient uptake, improved photosynthetic efficiency, and hormonal regulation mediated by the fungal filtrate. Collectively, these results demonstrate that fungal filtrate



Plate 2: Effect of thobroxide (fungal filtrate) compare to control on tuberization in potato

Notably, the effects of jasmonic acid (JA) and methyl-jasmonate (MeJA) on potato tuberization were studied concerning cytokinins using single-node cuttings (SNCs) *in vitro*. While jasmonates promoted root growth, BA inhibited root growth and counteracted the stimulatory effects of jasmonates. However, jasmonates did promote tuber growth after induction in early cultivars potentially due to their lower levels of endogenous gibberellins (Sarkar *et al.*, 2006) [18].

Conclusion

Jasmonic acid (JA), benzylaminopurine (BAP), and fungal filtrate significantly enhanced *in vitro* potato tuberization compared with the untreated control. Among the JA treatments, 0.5 ppm JA effectively promoted tuberization by increasing the percentage of tuberizing plants, tuber number per plant, and tuber fresh weight, demonstrating its crucial role in regulating tuber initiation and development. 2 ppm BAP produced the highest percentage of tuberizing plants and significantly improved tuber number and fresh weight, confirming the positive role of cytokinins in potato microtuber formation. Application of 20 mL fungal filtrate markedly improved tuberization parameters, indicating that fungal-derived metabolites can effectively stimulate potato microtuber development.

Jasmonic acid (JA), a plant hormone renowned for its diverse roles in stress responses, defense mechanisms and developmental processes has recently emerged as a focal point in the study of tuberization. Research findings indicate that, the application of 0.5 ppm JA exerts a pronounced stimulatory effect on potato tuberization. Similarly, a fungal extract from a fungus, *Lasiodiplodia theobromae* (known to contain Theobroxide which triggers JA pathway) also showed improved tuberization. The observed enhancement in tuberization parameters therefore, underscores the potential role of JA as a valuable tool in augmenting potato yield and tuber quality.

The promotive effect of the fungal filtrate is likely associated with the induction of endogenous jasmonic acid biosynthesis, possibly through fungal metabolites such as theobroxide that stimulate lipoxygenase-mediated jasmonate production. The positive effects of fungal filtrate on tuber number and tuber fresh weight suggest its potential as a sustainable biological elicitor for improving potato productivity under *in vitro* conditions. Overall, the study demonstrates that fungal filtrate represents a promising eco-friendly alternative to conventional plant growth regulators for enhancing potato microtuberization. Further studies involving the isolation and characterization of the active fungal metabolites and validation under greenhouse and field conditions are recommended before large-scale application.

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Conflict of interest

The authors disclose no conflict of interest

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