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Callus Induction from Anthers of *Cannabis sativa*

Michelle M. McDonald and Jessica D. Lubell-Brand
Department of Plant Science and Landscape Architecture, University of Connecticut, 1376 Storrs Road, Unit 4067, Storrs, CT 06269, USA

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Abstract. **The ability to conduct de novo plant regeneration from culturing anthers would benefit breeding to produce doubled haploids of cannabis (*Cannabis sativa*). In vitro callus induction from anthers of a tetraploid male cannabis genotype and subsequent callus development was studied over four experiments. Callus production was best under dark conditions compared with light conditions (40 μmol·m^{-2}·s^{-1}) from anthers cultured for 30 days on Driver and Kuniyuki Walnut medium with vitamins supplemented with 5 mg·L^{-1} metatopolin (MT) plus 0.5 mg·L^{-1} 2,4-dichlorophenoxyacetic acid (2,4-D) or naphthalene acetic acid or 0.5 mg·L^{-1} 2,4-D only. Exposing flowering microshoots to 4 °C before anther harvest did not benefit callus induction, and exposing excised flower buds to 4 °C reduced the induction rate, possibly because the floral tissue had desiccated or was damaged from the cold temperature. The inclusion of 2,4-D in the induction medium benefited callus greening after subculture to fresh medium and exposure to light. Induced calli transferred to medium with 2,4-D plus MT or benzyladenine developed roots and nodules. When the rate of 2,4-D in combination 2,4-D plus MT medium was reduced at the fifth subculture, a de novo shoot-like structure was observed. This is the first report of callus induction from cannabis anthers. A 40% callus induction rate can be expected when anthers are cultured in the dark for 30 days on medium containing 0.5 mg·L^{-1} 2,4-D and 5 mg·L^{-1} MT. These findings may be applied to diploid cannabis and suggest that successive modifications of the hormones in the medium may lead to a reliable system for de novo haploid plant generation from anther-derived calli.**

Introduction

Cannabis (*Cannabis sativa*) breeding would benefit from the ability to conduct de novo regeneration for gene transformation and editing (Ahsan et al. 2025). Unfortunately, cannabis is recalcitrant in tissue culture, which has limited the implementation of these breeding approaches (Bennur et al. 2025). Micropropagation from nodal stem pieces has been accomplished; however, microshoots often suffer culture decline and exhibit variable ex vitro rooting success (Kurtz et al. 2022; Lubell-Brand et al. 2021). Success with adventitious shoot regeneration in cannabis has been very limited (Sorokin and Kovalchuk 2025). For both micropropagation and de novo regeneration, success varies by cultivar (Borbas et al. 2023; Sorokin and Kovalchuk 2025).

Callus induction and organogenesis with cannabis have been studied using leaves, petioles, stems, cotyledons, hypocotyls, and flowers and different auxins and cytokinins alone and in combination (Ndlovu et al. 2024). Anthers may be a productive source for organogenesis in cannabis, and anther culture would allow for the development of doubled haploids for quantitative trait loci mapping and homozygous germ lines (Ahsan et al. 2025; Galán-Ávila et al. 2021). Anther culture has been accomplished for nonrecalcitrant plant species, with success often affected by the types, rates, and combinations of auxins and cytokinins included in the culture medium (Richa and Bhoj 2022). The pretreatment of flowers with cold temperatures has been shown to enhance anther culture success for several plants (Islam and Tuteja 2012). Losa et al. (2020) found that anthers from some tetraploid asparagus (*Asparagus* hybrids) were more responsive to anther culture than those from diploids.

The objective of our research was to induce callus and indirect organogenesis from anthers of cannabis. A male, tetraploid photoperiod-sensitive cannabis genotype was used because we have observed tetraploids to be more responsive to in vitro tissue culture and micropropagation than diploids. If androgenesis is achieved, then the methods used herein could be applied to diploid cannabis. A series of experiments were conducted to evaluate different combinations and concentrations of growth regulators. Anther culture response to exposing flowering microshoots and excised flower buds to cold temperature was also evaluated.

Materials and Methods

In vitro cultures of the male, tetraploid photoperiod-sensitive 'Kentucky Sunshine'

Table 1. Expt. conditions and growth regulators in Driver and Kuniyuki Walnut medium with vitamins at each subculture.

	Exposure to 4 °C	Callus induction environment	Callus induction		Subculture 1		Subculture 2		Subculture 3		Subculture 4		Subculture 5		Subculture interval (d)
			Growth regulator	Concn (mg·L^{-1})	Growth regulator	Concn (mg·L^{-1})	Growth regulator	Concn (mg·L^{-1})	Growth regulator	Concn (mg·L^{-1})	Growth regulators	Concn (mg·L^{-1})	Growth regulators	Concn (mg·L^{-1})	
Expt. 1	—	light or dark	2,4-D	1	—	—	—	—	—	—	—	—	—	—	—
	—		2,4-D + MT	0.5 + 5	—	—	—	—	—	—	—	—	—	—	—
	—		NAA + MT	0.5 + 5	—	—	—	—	—	—	—	—	—	—	—
	—		MT	5	—	—	—	—	—	—	—	—	—	—	—
Expt. 2	—	dark	2,4-D + MT	0.5 + 5	IBA	1	TDZ + MT	0.1 + 0.5	TDZ + MT	0.1 + 0.5	—	—	—	—	20
	—		NAA + MT	0.5 + 5	Charcoal	2000	TDZ	0.1	TDZ	0.1	—	—	—	—	20
Expt. 3	Flowering microshoot at 0 or 5 d	dark	2,4-D + MT	0.5 + 5	2,4-D + BA	0.1 + 0.5	2,4-D + BA	0.1 + 0.5	2,4-D + BA	0.1 + 0.5	2,4-D + BA	0.1 + 0.5	—	—	15
Expt. 4	Excised inflorescence at 0 or 5 d	dark	2,4-D + MT	0.5 + 5	2,4-D + MT	0.5 + 5	2,4-D + MT	0.5 + 5	2,4-D + MT	0.5 + 5	2,4-D + MT	0.5 + 5	2,4-D + MT	0.025 + 5	17

2,4-D = 2,4-dichlorophenoxyacetic acid; BA = benzyladenine; Concn = concentration; IBA = indole-3-butyric acid; MT = metatopolin; NAA = naphthalene acetic acid; TDZ = thidiazuron.

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J.D.L. is the corresponding author. E-mail: jessica.lubell@uconn.edu.

Table 2. In vitro callus formation from anthers of cannabis (*Cannabis sativa*) in response to growth regulators in Driver and Kuniyuki Walnut medium with vitamins and exposure of anthers to light during induction or flowering structures to 4 °C.

	Light ($\mu mol \cdot m^{-2} \cdot s^{-1}$) or 4 °C exposure (d)	Induction media			Anthers producing calli (%)	Callus width (mm)	Subculture 1 media			Green calli (%)	Subcultures 2 and 3 media		Callus description end of subculture 3
		Growth regulator	Concn ($mg \cdot L^{-1}$)	n[i]			Growth regulator	Concn ($mg \cdot L^{-1}$)	n[ii]		Growth regulator	Concn ($mg \cdot L^{-1}$)	
Expt. 1, Light													
	0	—	—	8	9 b[iii]	—	—	—	—	—	—	—	—
	40	—	—	8	19 a	—	—	—	—	—	—	—	—
	—	2,4-D	1.0	8	9 ab	—	—	—	—	—	—	—	—
	—	2,4-D + MT	0.5 + 5.0	8	25 a	—	—	—	—	—	—	—	—
	—	NAA + MT	0.5 + 5.0	8	21 ab	—	—	—	—	—	—	—	—
	—	MT	5.0	8	1 b	—	—	—	—	—	—	—	—
Expt. 2													
	—	2,4-D + MT	0.5 + 5.0	10	43 a	2.4 a	IBA	1.0	4	82 a	TDZ + MT	0.1 + 0.5	Green or tan; friable
	—	—	—	—	—	—	—	—	—	—	TDZ	0.1	Green or tan; friable
	—	—	—	—	—	—	Charcoal	2000	4	52 b	TDZ + MT	0.1 + 0.5	Green or tan; friable, compact or nodular
	—	—	—	—	—	—	—	—	—	—	TDZ	0.1	Green or tan; friable, compact or nodular
	—	NAA + MT	0.5 + 5.0	10	59 a	3.1 a	IBA	1.0	6	10 c	TDZ + MT	0.1 + 0.5	Tan; friable
	—	—	—	—	—	—	—	—	—	—	TDZ	0.1	Tan; friable
	—	—	—	—	—	—	Charcoal	2000	5	17 c	TDZ + MT	0.1 + 0.5	Tan or brown; friable
	—	—	—	—	—	—	—	—	—	—	TDZ	0.1	Tan or brown; friable
Expt. 3, Flowering microshoots													
	0	2,4-D + MT	0.5 + 5.0	10	48 a	2.0 a	2,4-D + BA	0.1 + 5.0	5	78 a	2,4-D + BA	0.1 + 5.0	Green or tan; friable, nodular or rooty
	5	2,4-D + MT	0.5 + 5.0	10	47 a	2.3 a	2,4-D + BA	0.1 + 5.0	5	68 a	2,4-D + BA	0.1 + 5.0	Green or tan; friable, nodular or rooty
Expt. 4, Excised inflorescences													
	0	2,4-D + MT	0.5 + 5.0	13	32 a	2.9 a	2,4-D + MT	0.5 + 5.0	10	89 a	2,4-D + MT	0.5 + 5.0	Green or tan; friable, nodular or rooty
	5	2,4-D + MT	0.5 + 5.0	7	2 b	2.4 a	2,4-D + MT	0.5 + 5.0	2	96 a	2,4-D + MT	0.5 + 5.0	Green or tan; friable or nodular

[i] Ten anthers/n.

[ii] Five calli/n.

[iii] Mean separation within columns within experiments (and within main effects, light and induction medium, for Expt. 1) indicated using different letters by Tukey's honestly significant difference test at $P \leq 0.05$.

2,4-D = 2,4-dichlorophenoxyacetic acid; BA = benzyladenine; Concn = concentration; IBA = indole-3-butyric acid; MT = metatopolin; NAA = naphthalene acetic acid; TDZ = thidiazuron.

S_1 × ('Candida' × 'Wife') were initiated using nodal stem pieces according to Lubell-Brand et al. (2021). Microshoots were exposed to a short photoperiod, according to the methods of McDonald and Lubell-Brand (2026), to produce aseptic flowers for anther extraction and culturing. Anthers were extracted from unopened flower buds, and anthers 1.5 to 3 mm in length were used for experiments. Four separate experiments were conducted and the growth regulators, exposure of flowering microshoots or excised flowers to cold temperature at 4 °C, incubation of anthers in the dark or light (at 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$) during callus induction, and subculture interval for each experiment are described in Table 1. Expt. 1 evaluated callus induction from anthers only, whereas Expts. 2 to 4 evaluated callus induction and development over three or more culture periods (Table 1). The experimental unit was a 60-mm-diameter plastic petri dish with anthers or calli. Petri dishes contained Driver and Kuniyuki Walnut medium with vitamins (Driver and Kuniyuki 1984), 3% sucrose, and 0.8% (w/v) agar at pH 5.7 plus any growth regulators or other supplements listed in Table 1. Anthers were set with their longest side against the medium surface. For each experiment, the number of anthers or calli per petri dish and number of replications are listed in Table 2. Experimental units were arranged in a completely randomized design and held in a growth chamber set at 25 °C with an 18-h photoperiod provided by white light-emitting diode lamps at an intensity of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except during callus induction under dark conditions, when the lights were off or blocked using blackout cloth. The number of anthers forming calli was counted 30 d after anthers were stuck, then anthers with calli were subcultured and exposed to light conditions. Before the second subculture, the number of calli that were green was counted. Before the fourth subculture, observations of callus color (green, tan, brown) and texture (friable, compact, nodular, rooty) were recorded. Data were subjected to an analysis of variance (PROC GLIMMIX) and mean separation with Tukey's honestly significant difference test ($P \leq 0.05$) using SAS v. 9.4 (SAS Institute, Cary, NC, USA). Main effects (light and induction media) are shown for Expt. 1, because the interaction was not significant (Table 2). The interaction of induction media × subculture 1 media is shown for Expt. 2.

Results and Discussion

Callus induction from anthers was accomplished for cannabis (Fig. 1). The induction media and procedure used, whereby anthers were harvested from in vitro flowering microshoots, was successful over a series of experiments (Table 1). In Expt. 1, twice as many anthers produced calli when incubated in the dark for 30 d compared with those incubated in the light (Table 2). Dark conditions also resulted in greater callus induction from cannabis leaves and petioles (Holmes et al. 2021). Other studies report callus induction for cannabis using light (Cheng et al. 2016; Lata et al. 2010;

Monthony et al. 2021; Thiry et al. 2026) or dark (Feeney and Punja 2003; Slusarkiewicz-Jarzina et al. 2005) conditions. Based on our finding, anthers were induced in dark conditions for all subsequent experiments.

The inclusion of both auxin and cytokinin in the culture medium is generally recommended for callus induction from plants (Hartmann et al. 2002; Hesami et al. 2023). Induction medium containing the auxin 2,4-dichlorophenoxyacetic acid (2,4-D) only or a combination of auxin [2,4-D or naphthalene acetic acid (NAA)] and the cytokinin metatopolin (MT) resulted in a greater percentage of anthers forming calli than medium containing MT only (Table 2). Previous studies report callus induction from cannabis hypocotyls and cotyledons using media containing NAA and the cytokinin thidiazuron (TDZ) (Chaohua et al. 2016; Sorokin and Kovalchuk 2025; Wielgus et al. 2008). Callus induction rates for Expts. 2 and 3 were greater than 40%, which was approximately double the best rate from Expt. 1 (Table 2). Variation among experiments is not unexpected and has been reported for callus induction from cannabis leaves (Page et al. 2021). For cannabis, callus induction rates of 60% to 80% have been found for hypocotyls (Sorokin and Kovalchuk 2025) and rates of 100% have been seen for petioles and leaves (Monthony et al. 2021; Slusarkiewicz-Jarzina et al. 2005).

The balance of auxin to cytokinin in the culture medium can affect shoot and/or root regeneration from callus (Hartmann et al. 2002). In general, a high cytokinin-to-auxin ratio will promote shoot formation; the reverse ratio will promote root formation (Hesami et al. 2023). Hormone influence on callus performance is affected by hormone concentration and mode of action. The hormone 2,4-D is a strong auxin compared with NAA, for example, because 2,4-D stimulates cell division, which results in high callus proliferation, whereas NAA stimulates cell elongation more than cell division (Thiry et al. 2026). Therefore, a greater concentration of NAA than 2,4-D would likely be necessary to influence cell division. In Expt. 2, more calli from the 2,4-D + MT induction medium developed a healthy green color (Eskandari et al. 2023) after the first subculture and exposure to light than calli from the NAA + MT induction medium (Table 2). This may have resulted from residual 2,4-D activity in the callus tissue that continued to impart a positive influence on callus performance. Charcoal was used in subculture 1 to dilute out auxin from the calli before exposure to cytokinins (TDZ or TDZ + MT) in subcultures 2 and 3, which we hoped would stimulate shoots, but did not. Lata et al. (2010) reported using TDZ for de novo shoot induction from cannabis leaf–derived calli; however, their result could not be reproduced by Monthony et al. (2021). Overall, charcoal did not benefit calli greening (Table 2). Calli induced on NAA + MT and subcultured to charcoal turned brown and died.

Callus induction and performance was not enhanced by the pretreatment of flowering microshoots with a cold temperature for 5 d (Table 2). Exposing excised flower buds to cold for 5 d reduced the ability of anthers to form calli, possibly because the floral tissue had desiccated or was damaged from the cold temperature. Most calli (≥ 68%) subcultured in a medium containing 2,4-D + MT or benzyladenine and exposed to light developed green coloration (Fig. 2). The calli grown on this media had a friable texture and produced

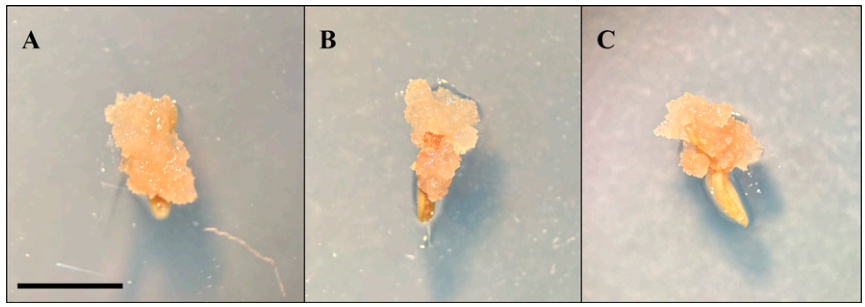

Fig. 1. Callus forming from anthers of tetraploid cannabis (*Cannabis sativa*) 'Kentucky Sunshine' S_1 × ('Candida' × 'Wife') after 30 d of dark incubation: anther 1 (**A**), anther 2 (**B**), and anther 3 (**C**). Scale bar = 3 mm.

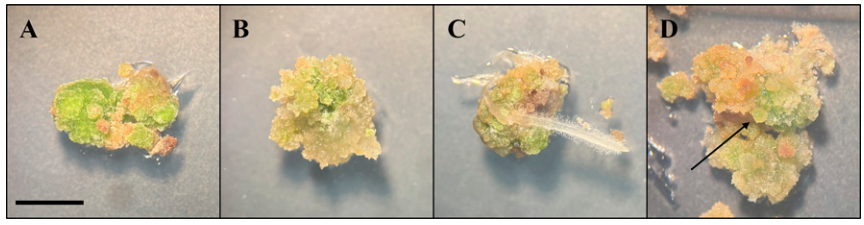

Fig. 2. Different textures of callus derived from anthers of cannabis (*Cannabis sativa*) 'Kentucky Sunshine' S_1 × ('Candida' × 'Wife'): compact (**A**), friable (**B**), rooty (**C**), and nodular (**D**). The arrow indicates a nodule. Scale bar = 5 mm.

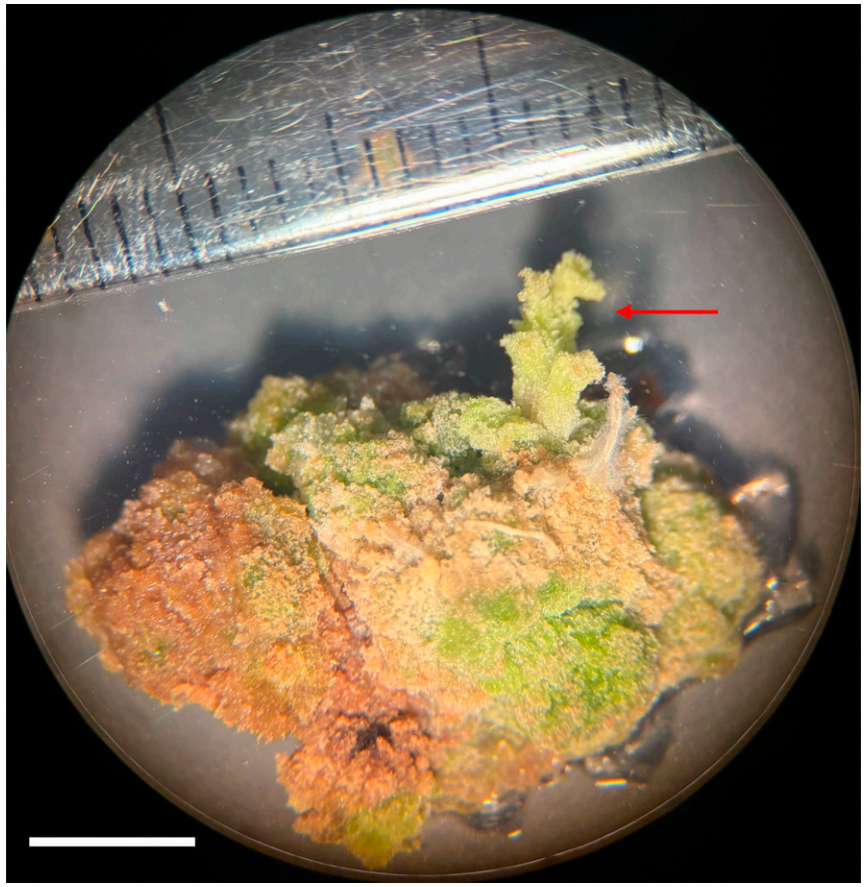

Fig. 3. Putative de novo shoot regenerated from anther-derived callus of cannabis (*Cannabis sativa*) 'Kentucky Sunshine' S_1 × ('Candida' × 'Wife'). Arrow indicates shoot. Scale bar = 5 mm.

de novo roots, which were observed between subcultures 2 and 3. Roots formed from regions of callus that were tan and friable. Feeney and Punja (2003) produced rooty calli from cannabis petioles using 2,4-D and kinetin. Nodular calli, which form meristematic centers (Slusarkiewicz-Jarzina et al. 2005), was observed in Expts. 3 and 4; however, these regions did not regenerate shoots (Fig. 2). A single shootlike structure was observed after subculture 5 when calli growing on 2,4-D + MT medium was transferred to medium with substantially less 2,4-D (at 0.025 mg·L^{-1}) plus the same rate of MT (Table 1; Fig. 3). The shoot was green and appeared to have a developed stem axis. Unfortunately, shortly after this discovery, the medium became contaminated and the shoot was lost.

Conclusion

To our knowledge this is the first report of callus induction from anthers of cannabis. Cannabis anthers cultured on Driver and Kuniyuki Walnut medium with vitamins containing 0.5 mg·L^{-1} 2,4-D + 5 mg·L^{-1} MT and incubated in dark conditions for 30 d can be expected to achieve a callus induction rate of ∼40%. We observed that the rate of callus induction from anthers declines as the time microshoots are in culture increases beyond ∼6 months. Culture decline is an issue for cannabis tissue culture and, as a result, cultures must be reinitiated in vitro more frequently than for other plants (Borbas et al. 2023; Lubell-Brand et al. 2021). Future research aimed at de novo shoot regeneration from anther-derived callus might consider reducing the concentration of auxin in the medium sooner than the fifth subculture period. It is likely that successive modifications of the hormones in the medium may lead to a reliable system for de novo shoot regeneration from anther-derived callus. Findings with tetraploid cannabis should be transferable to diploid genotypes.

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