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INVITED REVIEW

The status of *in vitro* regeneration and genetic transformation in the recalcitrant oil seed crop *Sesamum indicum* L

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Abstract

Sesame (*Sesamum indicum* L.) is the oldest important edible oilseed crop found throughout many tropical and subtropical regions of the world. India ranks second in its domestication with a total production of 0.67 million tons. The growth index of sesame in Asia, Africa, and South and Central America is 54.9%, 40.8%, and 4.3%, respectively. The crop has high economic potential but stress factors like temperature sensitivity, early senescence, pest attack, water logging, and disease infestations limit its productivity worldwide. Its recalcitrant nature, sexual incompatibility, and post fertilization barriers greatly restrict the generation of new varieties, *via* tissue culture and traditional breeding strategies. Thus, genetic engineering appears to be the best alternative to improve its yield by developing stress-tolerant plants. The callus induction and regeneration frequency in sesame is highly genotype dependent. Regeneration is observed in different cultivars *via* callus phase or directly from different explants mainly on Murashige and Skoog basal medium (MS) with high cytokinin and low auxin concentrations. The attempts towards developing genetic transformation protocols has resulted in very limited success. The present review highlights the history and discusses the detailed progress of sesame tissue culture and genetic transformation research with respect to genotype dependency, different medium compositions, plant hormones, and explant age.

Keywords *Sesamum indicum* · Recalcitrant · De-embryonated cotyledon · Shoots regeneration · Plant growth regulator

Introduction

The sesame (*Sesamum indicum* L.; 2n = 26) belongs to the family Pedaliaceae. According to Kobayashi *et al*. (1990), genus sesame comprises 36 species found mainly in Africa and Asia. Depending on the chromosome number, the thirty-six sesame species fall in three groups including 2n = 26, 32, and 64; however, the cytology of 12 species still needs to be studied (Nimmakayala *et al*. 2011). The archaeological findings revealed that cultivated sesame was derived from the wild species *S. malabaricum.* Sesame cultivation was established in South Asia at the time of the Harappan civilization and later spread west to Mesopotamia before 2000 B.C. (Fuller 2003). Sesame is cultivated worldwide, and the top ten sesame countries in terms of production are Sudan, India, China, Myanmar, Sudan (former), Nigeria, the United Republic of Tanzania, South Sudan, Ethiopia, and Uganda (FAO 2020). Globally, sesame is cultivated in 13.96 million hectares (mha) with a total production of 6.8 million tons. The sesame seed production index in Asia, Africa, and America is 53.1%, 42.5%, and 4.3%, respectively. Sudan ranks first with a production of 0.79 million tons, whereas India ranks second with 0.67 million tons (FAO 2021). India is the largest exporter of sesame seeds (Kumaraswamy *et al*. 2015), and the maximum sesame production was found in West Bengal followed by Gujarat state.

Sesame is an annual herb, completing its life cycle in 90 to 150 d, and reaches 60 to 120 cm in height with moderate branching or unbranched, ovate to lanceolate leaves with or without hairs and campanulate flowers varying from purple to white in color. The capsule size varies and possesses > 100 seeds, with seed color varying from black to white (Andrade *et al*. 2014). Sesame seeds contain 50 to 60% oil, 20% protein, and 13 to 14% carbohydrate (Morris 2002). Sesame, referred to as the

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"Queen of Oilseeds" (Lakhanpaul *et al*. 2012), is rich in oil and essential minerals and, thus, is largely (70%) employed for oil production and forms an important ingredient in cuisines, cosmetics, and medicines. The presence of antioxidants, lignins (sesamin and sesamolin), and tocopherols in sesame impart health-promoting attributes. The availability of antioxidants increases its demand as a food, enhances the shelf life, and reduces rancidity of the sesame oil (Dossa *et al*. 2017). The oil contains 35% monounsaturated fatty acids and 44% polyunsaturated fatty acids (Islam *et al*. 2016); it also contains other fatty acids, including oleic and linoleic acids, which constitute almost 40 to 45% each (Zhang *et al*. 2013), and palmitic and stearic acids (Kamal-Eldin et al. 1992). The roasting of sesame converts the sesamolin to sesamol, enhancing its antioxidant anticancer activities (Islam *et al*. 2016). The traditional methods of medicines in ayurveda, Chinese, and Tibetan forms consider sesame to be a vital source of anti-inflammatory, anti-proliferative, anti-hypertensive, anti-neurodegenerative, and anticancer constituents. Sesame has also attained interest in a wide commercial sector, as its leaves and roots are used in the production of hair dyes, in emollient plaster in Sri Lanka (Wesis 1971), and as a cattle feed from the oil cake that is produced.

Sesame production suffers heavy yield losses due to biotic factors (Tiwari *et al*. 2011), abiotic factors (Rao and Ravishankar 2002), indeterminate growth, uneven capsule ripening, and seed shattering. The pathogenic diseases like root or stem rot and phytophthora blight (Gangopadhyay *et al*. 1998) and charcoal rot by *Macrophomina phaseolina* fungus (Silme and Cagirgan 2010; Enikuomehin *et al*. 2011; Chowdhury *et al*. 2014) are serious threats to sesame production. It has been reported that by 2030 the sesame consumption would reach 100 million metric tons (Troncoso-Ponce *et al*. 2011). Therefore, it is important to develop sesame varieties for increasing seed yield, oil or fatty acid quality and quantity, functional bioactive compounds, and biotic and abiotic stress tolerance (Rao and Ravishankar 2002). Breeding efforts in sesame have focused on developing improved cultivars with traits, such as higher yield, disease resistance, drought tolerance, improved oil quality, and desirable agronomic characteristics (Teklu *et al*. 2022). The important aspect of breeding is genetic diversity; however, sesame is known for its narrow genetic base (Bhat *et al*. 1999), which poses challenges for breeders. To overcome this limitation, various approaches have been used to introduce genetic diversity into breeding populations, including the use of wild relatives, landraces, and diverse germplasm collections (Yermanos *et al*. 1972). These diverse genetic resources provide a valuable pool of traits that can be incorporated into cultivated sesame.

Traditional breeding methods, such as mass selection and pedigree breeding, have been employed to improve sesame cultivars (Tripathy *et al*. 2019). More recently, molecular breeding techniques have been applied to sesame breeding, allowing for more precise selection and faster progress. Molecular markers, such as simple sequence repeats (SSRs, Dixit *et al*. 2005; Spandana *et al*. 2012; Badri *et al*. 2014; Yan-Xin *et al*. 2014; Uncu *et al*. 2015; Wang *et al*. 2017) and single nucleotide polymorphisms (SNPs, Wei *et al*. 2014; Du *et al*. 2019), have been used for genetic analysis and marker-assisted selection (MAS; Wei *et al*. 2009; Ali *et al*. 2007) in sesame breeding programs. These techniques enable breeders to select plants with desired traits at the molecular level, facilitating more efficient and targeted breeding efforts.

The advancements in genomic technologies, including next-generation sequencing and genotyping-by-sequencing, have provided valuable genomic resources for sesame breeding. With the availability of assembled whole genome sequence of the *S. indicum* and detailed information of the oil biosynthetic pathways and stress-responsive genes (Wang *et al*. 2014, 2015, 2021; Dossa *et al*. 2017; Wei *et al*. 2017), it is possible to understand the different regulatory mechanisms and employ different genetic engineering techniques to enhance the economic potential of the sesame crop. The advantage of this highly important genome data can be very useful for the improvement of sesame crop either by overexpression for gain of function or editing advantageous genes by CRISPR-Cas9 or other molecular tools.

The recalcitrant nature of sesame significantly reduces the regeneration and genetic transformation efficiency (Baskaran and Jayabalan 2006; Zimik and Arumugam 2017). To date, the regeneration protocols with different cultivars of sesame are reported; however, only few reports with limited success on genetic transformation are available. In this review, we have highlighted the regeneration protocols developed with different varieties of sesame. The effect of major factors on regeneration efficiency in the sesame, like type of explants, age of explants, medium compositions, basal medium, and different hormone compositions, is discussed (Fig. 1). The review also emphasizes the efforts on sesame transformation, which are very miniscule and have limited success. The problems in sesame regeneration and genetic transformation are also discussed.

Plant regeneration

Plant tissue culture is the *in vitro* technique used to regenerate plants from different tissues and organs in sterile condition for better traits or a large number of genetically similar plants. Since the last couple of decades from the advent of the totipotency phenomenon, the tissue culture process has shown successful results in a large number of plants. Different methods, like micropropagation, somatic embryogenesis (SE), anther culture, meristem culture, and somaclonal and gametoclonal variations, have provided opportunities to develop the new varieties of plants. The

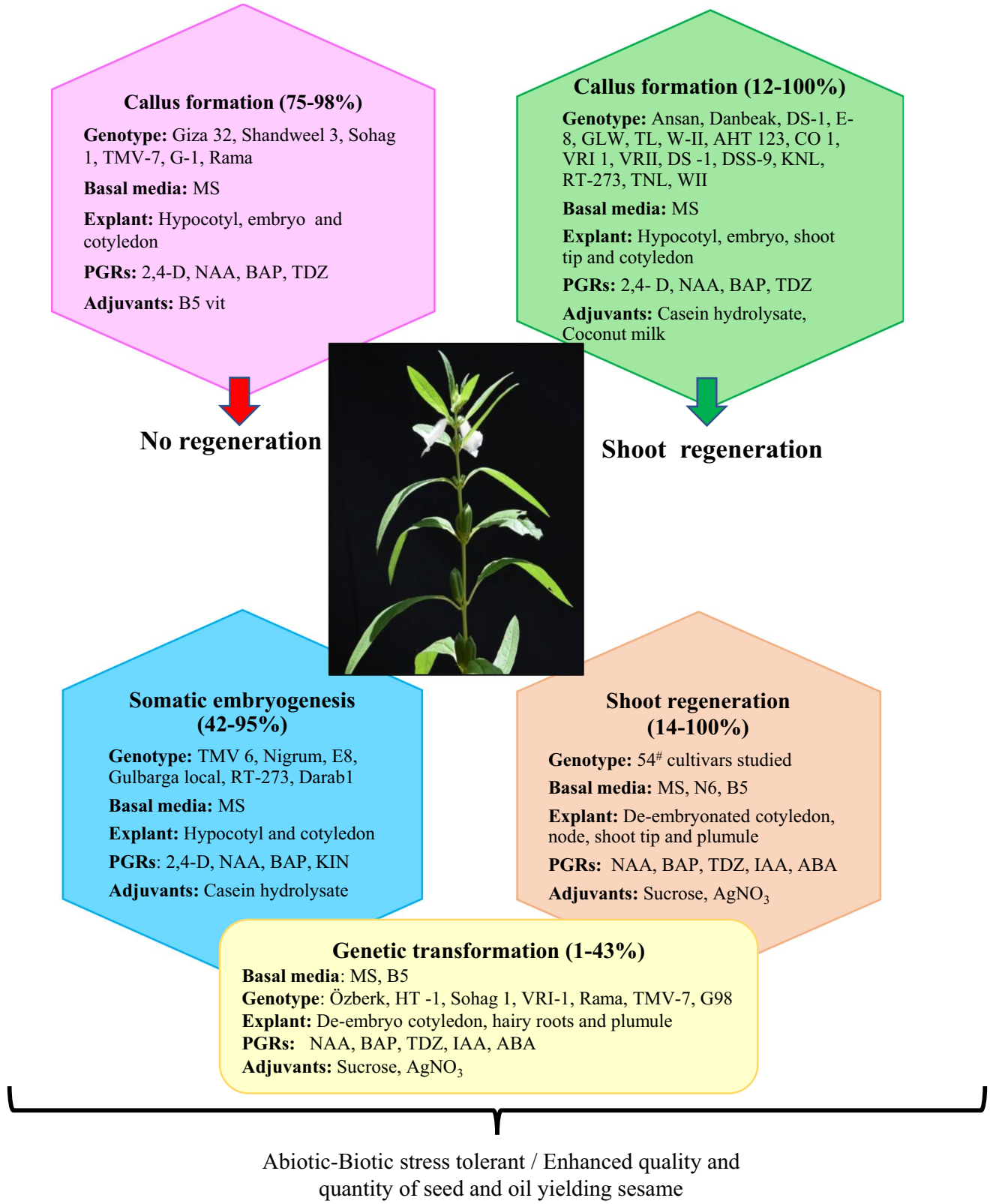

Figure 1. Schematic representation factors affecting callus formation, somatic embryogenesis, shoot regeneration and genetic transformation in *Sesamum indicum* L. # denotes following cultivars: Busia, Ex-El, Indian, Koyonzo, Mbale, McWhite, Mtwara-2, Siaya, Dasak, HT -1, TKG-55, Pb No. 1, GT-2 Himalayan, Sohag 1, SVPR – 1, DS-1, E-8, GLW, TLB, WII, DS-1, DSS-9, KNL, RT-273, TNL, WII, VRI-1, HT-1, DS-1, DSS-9, KNL, RT-273, TNL, WII, SVPR-1, TMV-7, AKT 64, Rajeshwari, RT127, TC 25, TMV 3, TMV 4, TMV 5, TMV 6, UMA, VRI1, TMV-3, JK-1, JT-7, PADMA, PHULE-TIL1, RT-103, TAPI-A, Rama, GT-3, GT-4.

regeneration of whole plant from single cell was reported over 50 yr ago by Steward *et al.* (1970). The success for regeneration of whole plant varies from species to species where the medium compositions, plant growth hormones, and other adjuvants play a major role. The high-frequency regeneration is a prerequisite for the improvement of different crops by genetic engineering. The regeneration protocols in different oleiferous species are developed for enhanced agriculture traits. In sesame, the regeneration protocols are highly dependent on different cultivars. The proper regeneration system is still a major drawback, and, therefore, genetic engineering of this crop has limited success (Were *et al.* 2006; Seo *et al.* 2007; Yadav *et al.* 2010; Chowdhury *et al.* 2014; Zimic and Arumugam 2017). Lee *et al.* (1985) published the first report on shoot regeneration from the shoot tip explant. Furthermore, George *et al.* (1987) showed regeneration in sesame *via* SE and multiple shoot production from shoot tips. Since then, sesame tissue culture has been reported using different explants to enhance shoot formation capacity (leaf, cotyledon, shoot tips, mature embryo, anther, hypocotyl, de-embryonated cotyledon, and plumule explant). The details of the regeneration protocols are discussed in the following sections.

Plant regeneration *via* somatic embryogenesis

In vitro SE is a developmental process in which a somatic cell can differentiate into non-zygotic embryos that can develop into a new plant under appropriate conditions. SE follows two main stages called induction and expression (Jimenez 2005). During the induction phase, cells pass through the physiological changes and altered gene expression for acquiring the embryogenic characteristics (Feher *et al.* 2002). Furthermore, in appropriate culture medium and plant growth regulators (PGRs), the induced cell develops into full embryos (Jimenez 2005). The somatic embryos (SEs) can be formed indirectly *via* callusing phase or directly without callusing phase. In sesame, different cultivars, like TMV 6, Nigrum, Darab 1, and E8, showed SEs. Different explants, like cotyledons, shoot tips, hypocotyls, and PGRs alone or in combinations, were used for the formation of SEs. In sesame until now, only five reports were published on SEs formation, where four reports show the SE *via* callus phase (Mary and Jayabalan 1997; Xu *et al.* 1997; Shashidhara *et al.* 2011; Chamandoosti 2016). Until now, the highest SE frequency was observed by Honnale and Rao (2013) directly from cotyledonary and hypocotyl explants from 5-d-old seedlings. The cotyledon explants showed a higher number of SEs compared to hypocotyls (Honnale and Rao 2013). The 95% cotyledon explants showed SE with a large number of SEs (59.16 ± 4.30) on 3.0 mg L^{-1} 2,4-D + 1.0 mg L^{-1} BAP (Honnale and Rao 2013; Table 1). The 2,4-D was found to be very efficient for induction of SEs compared to other auxins, and further addition of low concentrations of BAP enhanced the frequency of SE (Honnale and Rao 2013). It was observed that 2,4-D was the key PGR used in all the studies for embryo formation. In addition to 2,4-D, BAP, Kinetin, and NAA also helped in SEs formation in sesame. The addition of both 2,4-D and BAP is suggested in several reports as an important factor for inducing and developing SEs in different crops (Jimenez 2005).

Plant regeneration *via* callus induction

In sesame, different cultivars, like E-8, G-1, Giza 32, Rama, Sohag 1, Shandweel 3, and TMV-7, showed only callus induction, which eventually did not regenerate in shoot buds (Al-Shafeay *et al.* 2011; Pusadkar *et al.* 2015; Gayatri and Basu 2020; Table 2). Al-Shafeay *et al.* (2011) reported high-frequency callus induction from embryo, cotyledon, and hypocotyl explants in Giza 32, Sohag 1, and Shandweel 3 varieties. The callus cultures, when transferred on MS (Murashige and Skoog 1962) medium with BAP, Kinetin, and IAA, turned brown and did not support shoot induction. However, the de-embryonated cotyledon explants cultured on MS medium with BA and IAA directly regenerated shoots without callus phase (Al-Shafeay *et al.* 2011). Pusadkar *et al.* (2016) obtained callus in TMV 7 and G-1 varieties in both hypocotyl and cotyledon on MS medium with different combinations of PGRs. NAA (0.5 mg L^{-1}) and TDZ (1.0 mg L^{-1}) showed the highest callus percentage in both TMV 7 (93.3%) and G 1 (90%). Similarly, Gayatri and Basu (2020) reported the callus production using different concentrations of 2,4-D, Kinetin, and BAP in the variety Rama. The highest frequency of callus formation (approximately 89%) was found on MS medium supplemented with 2.0 mg L^{-1} 2,4-D and 1.5 mg L^{-1} BAP. In this case, also the cotyledon explants showed the highest callus formation as reported by Al-Shafeay *et al.* (2011). According to the findings presented in Table 2, it can be observed that the varieties listed do not yield shoots through callus. However, exceptions were found in the cases of Sohag 1 (Al-Shafeay *et al.* 2011) and Rama (Gayatri and Basu 2020) varieties, where direct regeneration was successfully accomplished (Table 4). It appears that PGRs are not solely responsible for further shoot regeneration in these varieties as callus obtained on combination of 2,4-D and BAP has shown shoot regeneration in other sesame varieties as discussed in the next section (Kwon *et al.* 1993; Saravanan and Nadarajan 2005). Therefore, it is apparent that the differential callus response is highly genotype dependent.

In sesame, different cultivars, like Ansan, AHT 123, CO-1, Danbeak, DS-1, DSS-9, E-8, GLW, KNL, RT-273, SVPR-1, TMV 3, TL, TNL, VRI 1, VRII, and W-II, showed callus induction, and, subsequently, shoot regeneration (Table 3). The callus induction was reported from 0- to 10-d-old seedlings, cotyledons, embryos, leaf, shoot tips, and hypocotyl explants (Table 3). In all the reports, the

Table 1. Effect of explant, hormones, and media adjuvants on somatic embryogenesis in different cultivars of *Sesamum indicum* L

S. No	Cultivars	Explants	Explant conditions	Plant growth regulators	Other adjuvants	Embryogenic frequency/No. of embryos	References
1	TMV 6	Hypocotyl	7-d-old seedlings	2,4-D (18.1 µM) + NAA (2.2 µM)	-	62.3%/9.4*	Mary and Jayabalan 1997
2	Nigrum	Cotyledon	6-d-old seedlings	2,4-D (0.5 mg L^{-1}) + BAP (0.5 mg L^{-1})	500.0 mg L^{-1} CH	42%	Xu *et al*. 1997
		Hypocotyl	6-d-old seedlings	2,4-D (0.5 mg L^{-1}) + BAP (0.5 mg L^{-1})	-	51%	
3	E8	Hypocotyl	7-d-old seedlings	2,4-D (2.0 mg L^{-1}), KIN (0.5 mg L^{-1}) — callus	-	66.6%	Shashidhara *et al*. 2011
4	Gulbarga local			2,4-D (2.0 mg L^{-1}), KIN (0.5 mg L^{-1}) — callus	-	50%	
5	RT-273			2,4-D (2.0 mg L^{-1}), KIN (0.5 mg L^{-1}) — callus	-	40%	
6	E8	Cotyledon	5-d-old seedlings	2,4-D (3.0 mg L^{-1}) + BAP (1.0 mg L^{-1})	-	95%/59*	Honnale and Rao 2013
		Hypocotyl	5-d-old seedlings	2,4-D (4.0 mg L^{-1})	-	80%/17*	
7	Darab1	Hypocotyl	7-d-old seedlings	2,4-D (3.0 mg L^{-1}) + KIN (0.5 mg L^{-1})	-	57%	Chamandoosti 2016

The basal medium used was MS. *CH* casein hydrolysate, *KIN* kinetin. *Denotes number of somatic embryos per explant

Table 2. Callus formation from different cultivars of *Sesamum indicum* L

S. No	Cultivars	Explants	Explant conditions	Plant growth regulators	Other adjuvants	Frequency	References
1	Giza 32	Cotyledon	0-d-old seedlings	2,4-D (0.4 mg L^{-1})	B5 vit	74.8%	Al-Shafeay *et al*. 2011
		Embryo	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	90.7%	
		Hypocotyl	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	64.8%	
2	Shandweel 3	Cotyledon	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	97.2%	
		Embryo	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	89.2%	
		Hypocotyl	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	95.7%	
3	Sohag 1	Cotyledon	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	92.5%	
		Embryo	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	97.7%	
		Hypocotyl	0-d-old seedlings	2,4-D (0.5 mg L^{-1})	B5 vit	96.3%	
4	TMV-7	Hypocotyl	14-d-old seedlings	TDZ (1.0 mg L^{-1}) + NAA (0.5 mg L^{-1}) — callus	-	93.3%	Pusadkar *et al*. 2015
5	G-1	Hypocotyl	14-d-old seedlings	TDZ (1.0 mg L^{-1}) + NAA (0.5 mg L^{-1}) — callus	-	90%	
6	Rama	Cotyledon	2-d-old seedlings	2,4-D (2.0 mg L^{-1}), BAP (1.5 mg L^{-1}) — callus	-	88. 9%	Gayatri and Basu 2020

B5 Gamborg medium (Gamborg *et al.* 1968)

calluses were obtained on different auxins (2,4-D, IAA, and NAA) at variable concentrations. When these calluses were transferred on low concentration of auxin along with high concentration of BAP, the multiple shoots were observed. Kwon *et al*. (1993) reported the highest number of shoots per explant (2 to 13) from the callus explant on casein hydrolysate (CH)-supplemented medium. In contrast, other studies have reported significantly low rates of regeneration (1 to

Table 3. Effect of different hormones and other factors on shoot regeneration *via* callus formation in different cultivars of *Sesamum indicum* L

S. No	Cultivars	Explants	Explant conditions	Plant growth regulators	Other adjuvants	Callus formation %/number of shoots	Reference
1	Ansan	Cotyledon	5–7-d-old seedlings	NAA (2.0 mg L^{-1}) + BAP (0.2 mg L^{-1}) — callus	-	96%	Kwon *et al*. 1993
			1-m-old callus	BAP (2.0 mg L^{-1}) + NAA (0.1 mg L^{-1}) — shoots	CH (2.0 g L^{-1})	16%/2*	
		Hypocotyl	5–7-d-old seedlings	NAA (2.0 mg L^{-1}) + BAP (0.6 mg L^{-1}) — callus	-	96%	
			1-m-old callus	BAP (3.0 mg L^{-1}) + NAA (0.1 mg L^{-1}) — shoots	CH (2.0 g L^{-1})	36%/10*	
2	Danbeak	Cotyledon	5–7-d-old seedlings	2,4-D (2.0 mg L^{-1}) + BAP (0.4 mg L^{-1}) — callus	-	98%	
			1-m-old callus	BAP (4.0 mg L^{-1}) + NAA (0.1 mg L^{-1}) — shoots	CH (2.0 g L^{-1})	12%/4*	
		Hypocotyl	5–7-d-old seedlings	NAA (2.0 mg L^{-1}) + BAP (0.2–0.6 mg L^{-1}) — callus	-	100%	
			1-m-old callus	BAP (2.0 mg L^{-1}) + NAA (0.1 mg L^{-1}) — shoots	CH (2.0 g L^{-1})	44%/13*	
3	DS-1	Hypocotyl	0-d-old seedlings	MS — callus	-	-	Wadeyar *et al*. 2013
			30-d-old callus	TDZ (25.0 µM) + IAA (3.0 µM) — shoots	-	83.3%/2*	
4	E-8	Hypocotyl	0-d-old seedlings	MS — callus	-	-	
			30-d-old callus	TDZ (25.0 µM) + IAA (3.0 µM) — shoots	-	58%/1.5*	
5	GLW	Hypocotyl	0-d-old seedlings	MS — callus	-	-	
			30-d-old callus	TDZ (25.0 µM) + IAA (3.0 µM) — shoots	-	41.6%/1.6*	
6	TL	Hypocotyl	0-d-old seedlings	MS — callus	-	-	
			30-d-old callus	TDZ (25.0 µM) + IAA (3.0 µM) — shoots	-	58%/1.8*	
7	W-II	Hypocotyl	0-d-old seed	MS — callus	-	-	
			30-d-old callus	TDZ (25.0 µM) + IAA (3.0 µM) — shoots	-	41.6%/1.6*	
8	AHT 123	Embryo	-	2,4-D (3.5 mg L^{-1}) — callus	CH (0.1 g L^{-1})	57.5%	Saravanan and Nadarajan 2005
			-	IAA (0.5 mg L^{-1}) + BAP (1.0–1.5 mg L^{-1}) + KIN (1.25 mg L^{-1}) — shoots	-	-/6.00*	
9	CO 1	Embryo	-	2,4-D (3.0 mg L^{-1}) — callus	CM (0.1 g L^{-1})	62.8%	
			-	IAA (0.5 mg L^{-1}) + BAP (1.0 mg L^{-1}) + KIN (1.25 mg L^{-1}) — shoots	-	-/6.2*	
10	TMV 3	Embryo	-	2,4-D (3.5 mg L^{-1}) — callus	CM (0.1 g L^{-1})	62.1%	
			-	IAA (0.5 mg L^{-1}) + BAP (1.0–1.5 mg L^{-1}) + KIN (1.25 mg L^{-1}) — shoots	-	-/6.1*	
11	VRI 1	Embryo	-	2,4-D (3.0 mg L^{-1}) — callus	CM (0.1 g L^{-1})	64.9%	

Table 3. (continued)

S. No	Cultivars	Explants	Explant conditions	Plant growth regulators	Other adjuvants	Callus formation %/number of shoots	Reference
			-	IAA (0.5 mg L^{-1}) + BAP (1.0–1.5 mg L^{-1}) + KIN (1.25 mg L^{-1}) — shoots	-	-/5.16*	
12	VRII	Shoot tip	10-d-old seedlings	KIN (4.6 µM) + BAP (35.5 µM) — callus and shoots	-	100/11.5*	Baskaran and Jayabalan 2006
13	DS-1	Hypocotyl	7-d-old seedlings	KIN (1.5 mg L^{-1}) + NAA (0.5 mg L^{-1}) + BAP (1.5 mg L^{-1}) — callus	-	81.7%	Savitha *et al*. 2016
			2-m-old callus	KIN (1.0 mg L^{-1}) — shoots	-	91.7%/1.9*	
14	DSS-9	Hypocotyl	7-d-old seedlings	KIN (1.5 mg L^{-1}) + NAA (0.5 mg L^{-1}) + BAP (1.5 mg L^{-1}) — callus	-	73.3%	
			2-m-old callus	KIN (1.0 mg L^{-1}) — shoots	-	83.3%/1.8*	
15	KNL	Hypocotyl	7-d-old seedlings	KIN (1.5 mg L^{-1}) + NAA (0.5 mg L^{-1}) + BAP (1.5 mg L^{-1}) — callus	-	68.3%	
			2-m-old callus	KIN (1.0 mg L^{-1}) — shoots	-	75%/1.7*	
16	RT-273	Hypocotyl	7-d-old seedlings	KIN (1.5 mg L^{-1}) + NAA (0.5 mg L^{-1}) + BAP (1.5 mg L^{-1}) — callus	-	70.8%	
			2-m-old callus	KIN (1.0 mg L^{-1}) — shoots	-	100%/2.5*	
17	TNL	Hypocotyl	7-d-old seedlings	KIN (1.5 mg L^{-1}) + NAA (0.5 mg L^{-1}) + BAP (1.5 mg L^{-1}) — callus	-	65%	
			2-m-old callus	KIN (1.0 mg L^{-1}) — shoots	-	58.3%/1.6*	
18	WII	Hypocotyl	7-d-old seedlings	KIN (1.5 mg L^{-1}) + NAA (0.5 mg L^{-1}) + BAP (1.5 mg L^{-1}) — callus	-	75.8%	
			2-m-old callus	KIN (1.0 mg L^{-1}) — shoots	-	66.7%/1.7*	

*Denotes number of shoots per explant. *CH* casein hydrolysate, *CM* coconut milk, *KIN* kinetin

2 shoots per callus explant) were observed, indicating the highly challenging and recalcitrant nature of sesame towards plant regeneration. Casein hydrolysate is considered rich in minerals, microelements, and vitamins and eliminates the problem of phosphate deficiency in the regenerating explants. The variable response towards shoot regeneration could be due to varietal differences and the endogenous auxin concentrations between genotypes (Khemkladngoen *et al*. 2011; Zimik and Arumugam 2017). The regeneration of shoots from the callus tissue after transferring on BAP medium is in agreement with other previously published reports from different crops species, like *Malus domestica* (Caboni *et al*. 2000), *Holostemma ada-kodien* (Martin 2002), and *S. indicum* cultivar SVPR-1 (Raja and Jayabalan 2010).

Plant regeneration *via* direct shoot induction/shoot morphogenesis

The regeneration *via* callus formation can lead to somaclonal variation, and moreover, the transformation is difficult *via* callus phase; therefore, direct regeneration was attempted using different cultivars in sesame (SVPR-1, WII, DS-1, E-8, GLW, TLB, and RT-273; Table 4). Explants, like cotyledons,

Table 4. Effect of different hormones and other factors on direct *in vitro* shoot regeneration in different cultivars of *Sesamum indicum* L

S. No	Cultivars	Explants	Basal media	Explant conditions	Plant growth regulators	Other adjuvants	Frequency (%)/ No. of shoots	References
1	Busia	Cotyledon	MS and N6 macronutrients	3-4-d-old seedlings	TDZ (20.0 µM) + IAA (2.5 µM)	-	45%/1.9*	Were *et al.* 2006
2	Ex-El						63%/4.4*	
3	Indian						45.6%/1.9*	
4	Koyonzo						53%/1.9*	
5	Mbale						43%/2*	
6	McWhite						51%/1.8*	
7	Mtwara-2						50%/2.7*	
8	Siaya						39%/2.2*	
9	Dasak	De-emb cot	MS	40-d-old immature seeds after flowering	BAP (22.2 µM) + IAA (5.7 µM)	-	17%	Seo *et al.* 2007
					BAP (22.2 µM) + IAA (5.7 µM) + ABA (3.8 µM)	$AgNO_3$ (29.4 µM)	50%	
10	HT-1	Cotyledon	MS	2-d-old seed	BAP (25.0 µM)	-	88%/9.3*	Yadav *et al.* 2010
		Cot node					70%/3.6*	
11	TKG-55	Cotyledon					80%/3.6*	
12	Pb No. 1						80%/2.5*	
13	GT-2 Himalayan						80%/1.5*	
14	Sohag 1	Cotyledon	MS and B5 Vit	Mature seed	BAP (2.0 mg L^{-1}) + IAA (1.0 mg L^{-1})	$AgNO_3$ (5 mg L^{-1})	13.8%/20.4*	Al-Shafeay *et al.* 2011
15	SVPR-1	Shoot tip	MS	7-d-old seedlings	BAP (2.0 mg L^{-1}) + NAA (0.3 mg L^{-1})	-	91.8%/25.9*	Raja and Jayabalan 2011
		Node explant			BAP (2.5 mg L^{-1}) + NAA (0.4 mg L^{-1})		60.3%/20.4*	
16	DS-1	De-emb cot	½ MS	0-d-old seedlings	TDZ (20.0 µM) + IAA (2.5 µM)	-	80%/8.5*	Lokesha *et al.* 2012
17	E-8						77.8%/6.4*	
18	GLW						57.8%/5.5*	
19	TLB						66.7%/6*	
20	WII						84.4%/8.9*	
21	DS-1	De-emb cot	½ MS	0-hr-old seed	TDZ (20.0 µM) + IAA (2.5 µM)	-	100%/3.9*	Malaghan *et al.* 2013
22	DSS-9				TDZ (20.0 µM) + IAA (2.5 µM) + BAP (25.0 µM)		73.3%/2.6*	

Table 4. (continued)

S. No	Cultivars	Explants	Basal media	Explant conditions	Plant growth regulators	Other adjuvants	Frequency (%)/ No. of shoots	References
23	KNL						88.9%/7.6*	
24	RT-273						100%/8.2*	
25	TNL						88.9%/5.7*	
26	WII						42%/1.4*	
27	VRI-1	De-emb cot	MS	0-d-old seed	BAP (30.0 µM) + IAA (5.7 µM) + ABA (4.0 µM)	Sucrose (3–9%), $AgNO_3$ (30 µM)	57.3%	Chowdhury *et al.* 2014
28	HT-1	Cotyledon	MS	2-d-old Seedlings	BA (25 µM)	-	25%	Kapoor *et al.* 2015
29	DS-1	De-emb cot	½ MS	0-hr-old seedlings	TDZ (20.0 µM) + IAA (2.5 µM)	-	100%/6.0*	Malaghan 2016
30	DSS-9				TDZ (20.0 µM) + IAA (2.5 µM) + BAP (25.0 µM)		73.3%/6.4*	
31	KNL						88.9%/4.8*	
32	RT-273						100%/7.6*	
33	TNL						88.9%/6.0*	
34	WII						42%/3.4*	
35	SVPR-1	De-emb cot	MS	0-hr-old seedlings	BAP (2.0 mg L^{-1}) + IAA (0.5 mg L^{-1}) + ABA (0.5 mg L^{-1})	Sucrose 6%, $AgNO_3$ (0.25 mg L^{-1})	65%/13.3*	Pusadkar *et al.* 2016
36	TMV-7						67.3%/15.6*	
37	AKT 64	De-emb cot	MS	4-hr-old seed	BAP (6.5 mg L^{-1}) + IAA (1.0 mg L^{-1}) + $AgNO_3$ (5.0 mg L^{-1})	$AgNO_3$ (5 mg L^{-1})	10%	Zimik and Arumugam 2017
38	Rajeshwari						15.5%	
39	RT127						11.6%	
40	TC 25						8.3%	
41	TMV 3						20.5%	
42	TMV 4						14.4%	
43	TMV 5						15.5%	
44	TMV 6						18.3%	
45	UMA						34.7%	
46	VRI1						12.2%	
47	TMV-3	Cotyledon	MS	7–8-d-old seedlings	BAP (2.0 mg L^{-1})	-	74%/4.5*	Anandan *et al.* 2018

Table 4. (continued)

S. No	Cultivars	Explants	Basal media	Explant conditions	Plant growth regulators	Other adjuvants	Frequency (%)/ No. of shoots	References
48	JK-1	De-emb cot	MS	2-d-old seedlings	BAP (33.33 µM) + IAA (2.85 µM) + $AgNO_3$ (29.43 µM) + ABA (3.78 µM)		94.1%/5.3*	Debnath *et al.* 2018
47	JT-7						83%/4.2*	
48	PADMA						57.8%/3.2*	
49	PHULE-TIL1						68.9%/3.7*	
50	RT-103						77.1%/4.6*	
51	TAPI-A						60.8%/3.9*	
52	Rama	Plumule	MS, B5, N6, and SH	2-d-old seedlings	½ MS macro + ½ B5 macro + MS micro and vit + BAP (0.25 mg L^{-1})	-	94.5%	Gayatri and Basu 2020
					BAP (0.1 mg L^{-1}) + TDZ (1.0 mg L^{-1}) -shoots		-/16*	
53	GT-3	De-emb cot	MS	0-d-old seedlings	BAP (25.0 µM) + IAA (2.0 µM) + $AgNO_3$ (30.0 µM) + (ABA (4.0 µM)	$AgNO_3$ (30.0 µM)	83.3%/5.9*	Rajput *et al.* 2022
54	GT-4	De-emb cot	MS	0-d-old seedlings	BAP (25.0 µM) + IAA (2.0 µM) + $AgNO_3$ (30.0 µM) + (ABA (4.0 µM)	$AgNO_3$ (30.0 µM)	70%/5.5*	

The basal medium used was MS; however, Gayatri and Basu 2020 used MS, B5, N6 (Chu *et al.* 1975), and SH (Schenk and Hildebrandt 1972) as basal medium

De-emb cot de-embryonated cotyledon. *Denotes number of shoots per explant

de-embryonated cotyledons, cotyledonary nodes, nodes, shoot tips, plumule, hypocotyls, and PGRs, alone or in combinations were used for direct shoot induction (Fig. 1). For the majority, regeneration was achieved from cotyledons and de-embryonated cotyledons (Table 4). From the plumule explants, high-frequency direct shoot regeneration (94.44%) and the maximum number of shoots per explant (15.96) were achieved in the Rama cultivar (Gayatri and Basu 2020). Malaghan *et al*. (2013) achieved the highest shoot regeneration, for example, 100% (½ MS with 20.0 µM TDZ, 2.5 µM IAA, and 25.0 µM BAP) with 8.15 shoots per cotyledon in RT-273 cultivar. Despite reports of regeneration in various media supplemented with TDZ and IAA (Were *et al*. 2006; Seo *et al*. 2007; Al-Shafeay *et al*. 2011; Wadeyar *et al*. 2013) as well as BAP and IAA (Were *et al*. 2006), the overall frequency of regeneration remains low. As a result, researchers have also explored the use of adjuvants to enhance the efficiency of regeneration.

Effect of $AgNO_3$ on regeneration

In this context, fortification of MS medium with various concentrations of $AgNO_3$ along with BAP and IAA improved the frequency of regeneration (Table 4). $AgNO_3$ is used as an ethylene action blocker in *in vitro* cultures (Mohiuddin *et al*. 1997). Many plants, including sesame (Seo *et al*. 2007; Abdellatef *et al*. 2010; Al-Shafeay *et al*. 2011), have shown the ability of $AgNO_3$ to enhance *in vitro* regeneration (Williams *et al*. 1990; Ashwani *et al*. 2017; Panigrahi *et al*. 2017). Low concentrations of silver ions inhibited the impact of ethylene on plant cells by likely substituting the copper co-factor of the cell's ethylene receptor (ETR1) and rendering it resistant to ethylene, as previously demonstrated (Moshkov *et al*. 2008; Kumar *et al*. 2009).

The application of $AgNO_3$ dramatically accelerated regeneration in sesame (Seo *et al*. 2007; Chowdhury *et al*. 2014; Zimik and Arumugam 2017; Debnath *et al*. 2018; Rajput *et al*. 2022; Table 4). In addition, several other crops, including *Coffea camephora* (Kumar *et al*. 2007), *Zea mays* (Songstad *et al*. 1988), *Cucumis melo* (Roustan *et al*. 1992), *Brassica campestris* (Zhang *et al*. 1998), *Brassica juncea* (Pua and Chi 1993), and *Capsicum annuum* (Hyde and Phillips 1996), showed improved organogenesis from the addition of $AgNO_3$.

Effect of sucrose on regeneration

In the development of shoots, carbohydrates have been shown to serve as both an osmoticum and an energy source (Brown *et al*. 1979). Different investigations have shown the specific physiological role of sucrose in the induction of shoots (Brown *et al*. 1979; Strickland *et al*. 1987; Ramage and Leung 1996). In *Capsicum annuum* hypocotyl explants, an external source of sucrose is required for at least the first 4 d of cultivation (Ramage and Leung 1996). In *Aloe saponaria*, shoot organogenesis required a 4% sugar content (Kim *et al*. 2016). In sesame, the regeneration frequency improved in the presence of high sucrose concentrations in the medium (6 to 9%; Seo *et al*. 2007; Chowdhury *et al*. 2014; Pusadkar *et al*. 2016; Debnath *et al*. 2018; Table 4). High sucrose pre-treatment in these studies has enhanced adventitious shoot production by resulting in high sucrose uptake in explants. Generally, the explants are pre-cultured on high sucrose (6 to 9%) medium for 7 to 15 d and then transferred on 3% sucrose. According to Seo *et al*. (2007), pre-culturing cotyledon explants for 2 wk on 9% sucrose and then sub-culturing to medium containing 3% sucrose significantly improved adventitious shoots production in sesame; however, prolonged incubation on 9% was not useful and explants turned brown. According to Chowdhury *et al*. (2014) and Debnath *et al*. (2018), the addition of sucrose along with ABA in the culture medium promoted regeneration. It was discussed that ABA might be facilitating the uptake of sucrose, and interestingly, both ABA and sucrose synergistically improved adventitious shoot formation (Seo *et al*. 2007). However, the detailed experiments are required to prove and justify the role of ABA in sucrose uptake in sesame explants.

Effect of ABA on regenerations

Abscisic acid (ABA) is an important plant hormone, which plays a pivotal role in embryo and seed maturation (Zeevaart and Creelman 1988). It prevents the precocious germination of embryos in developing seeds. According to Choi and Jeong (2002) and García-Martín *et al*. (2005), ABA pre-treatment prevents premature germination of somatic embryos and decreases the production of secondary embryos. ABA helps the plants by protecting cells from desiccation during water limitation by regulating different genes and stomatal regulation and provides drought tolerance (Wasilewska *et al*. 2008). The role of ABA in promoting regeneration frequency in sesame has been reported by different researchers. In sesame, a brief pre-treatment of different durations with ABA increased the development of adventitious shoots (Seo *et al*. 2007; Chowdhury *et al*. 2014; Pusadkar *et al*. 2016; Debnath *et al*. 2018; Rajput *et al*. 2022; Table 4). The addition of ABA further to $AgNO_3$-supplemented medium showed enhanced regeneration efficiency in some reports (Debnath *et al*. 2018; Rajput *et al*. 2022). In most of the cases, the ABA pre-treatment for 1 wk promoted the regeneration efficiency (Table 4). The presence of ABA attributed to high sucrose uptake in explants and increased cellular sucrose content (Debnath *et al*. 2018). This is in agreement to the report of Seo *et al*. (2007) where the initial incubation of

cultures for 2 wk at high sucrose concentration increased adventitious shoot formation in sesame. The presence of ABA synchronizing the sucrose uptake is also reported in strawberry (Archbold 1988), pea (Estruch *et al*. 1989), and tobacco and beet (Saftner and Wyse 1984). It is well known that ABA promotes the uptake of sucrose by *Beta vulgaris* in root tissue (Saftner and Wyse 1984).

Root induction

The *in vitro* raised adventitious shoots of different cultivars of sesame that were transferred on a rooting medium supplemented with different auxins, like IBA, IAA, and NAA, at different concentrations formed roots (Table 5). Different cultivars showed different root frequency; in some, the rooting percentage was < 50% whereas in other cultivars, like Dasak, Uma, JK-1, TMV3, GT-3, and GT-4, the root frequency was > 50%. In cultivar Dasak, high-frequency root formation (98%) was observed on MS media supplemented with 2.69 µM NAA (Seo *et al*. 2007), but the highest number of roots per explant (13.81) was obtained by Saravanan and Nadarajan (2005). Gayatri and Basu (2020) observed that the addition of NAA or IAA to basal medium did not help in root formation, but it did support callus formation, which affected shoot growth negatively followed by shoot fatality. Similarly, in the present study, no root formation was observed in transgenic plants of cultivars GT3 and GT4, and the basal end of the plants turned brown leading to plant death during subsequent culturing. Gayatri and Basu (2020) explained that half concentration of MS macronutrients in combination with SH (Schenk and Hildebrandt 1972)

Table 5. Root induction response on different PGRs of *Sesamum indicum* L

S. No	Cultivars	Basal media	Plant growth regulators	Root frequency/ No. of roots	References
1	CO 1	MS	IBA (1.0 g L^{-1}) + IAA (1.25 mg L^{-1})	-/13.81*	Saravanan and Nadarajan 2005
2	Mtwara-2	N_6	BAP (20.0 µM) + NAA (1. µM)	36.7%/12.8*	Were *et al*. 2006
3	-	MS	NAA (8.0 µM)	-	Baskaran and Jayabalan 2006
4	Dasak	MS	NAA (2.7 µM)	98%	Seo *et al*. 2007
5	HT-1	MS	IBA (2.0 µM)	41.6%	Yadav *et al*. 2010
6	Sohag-1	MS + B_5 vit	IAA (1.0 mg L^{-1})	-	Al-Shafeay *et al*. 2011
7	SVPR-1	MS + B_5 vit	NAA (1.5 mg L^{-1}) + BAP (0.03 mg L^{-1})	68.1%/4.8*	Raja and Jayabalan 2011
8	-	MS	NAA (2.7 µM)	-	Lokesha *et al*. 2012
9	E-8	½ MS	½ MS medium	40–50%	Honnale and Rao 2013
10	VRI-1	MS	IAA (4.57 µM)	-	Chowdhury *et al*. 2014
11	HT-1	MS	IBA (2.0 µM)	40%	Kapoor *et al*. 2015
12	DS-1	½ MS	NAA (2.7 µM)	27.8%	Malaghan 2016
13	DSS-9			24%	
14	KNL			33.3%	
15	RT-273			53.3%	
16	TNL			27.5%	
17	W II			32%	
18	Darab1	MS	NAA (1.5 mg L^{-1}) + BAP (0.03 mg L^{-1})	-	Chamandoosti 2016
19	DS-1	MS	NAA (2.7 µM)	40%/1*	Savitha *et al*. 2016
20	DSS-9			33.3%	
21	KNL			12.5%	
22	RT-273			50%/1*	
23	TNL			14.3%	
24	W II			28.6%	
25	Uma	MS	IBA (1.0 mg L^{-1})	76.3%/7*	Zimik and Arumugam 2017
26	JK-1	MS	NAA (2.69 µM)	66.7%/5.9	Debnath *et al*. 2018
27	TMV3	MS	IBA (0.5 mg L^{-1})	70%/4.2*	Anandan *et al*. 2018
28	Rama	MS + SH	½ MS macro + SH (micro and vit.)	97.3%/6.2*	Gayatri and Basu 2020
29	GT-3	MS	MS + NAA (2.0 µM)	70%/5.4*	Rajput *et al*. 2022
30	GT-4			66.7%/5.2*	

*Denotes number of roots per explant. The reports wherein the data of rooting frequency is not given are marked with -

micronutrient and vitamins supported better root frequency compared to full-strength MS major. This suggests that reduced salt concentration is necessary for high frequency of root formation in the cultivar Rama.

Agrobacterium-mediated transformation in sesame

As mentioned above, sesame is a highly important oil seed crop, and it faces a major problem of abiotic and biotic stresses. Therefore, a need for genetic improvement lies in this crop towards the development of disease-resistant and nutritionally enriched varieties. The sexual incompatibility between the cultivated and wild species in sesame crop limits its improvement *via* conventional breeding method (Tiwari *et al*. 2011; Kulkarni *et al*. 2017). Genetic engineering of crops *via* overexpression, CRISPR-Cas9, and RNAi, has emerged as a potential tool for targeted changes for crops improvement.

The limited success of regeneration was discussed in the previous section. Because of unavailability of suitable and reproducible regeneration and transformation protocols, the success of genetic engineering in this crop remains a bottleneck (Zimik and Arumugam 2017). Until now, only a few research publications have reported on the genetic transformation of the sesame crop using *Agrobacterium*-mediated transformation (Table 6). Taskin *et al*. (1999) attempted the first *Agrobacterium*-mediated transformation in cultivar Ozberk using pBI121 vector; however, no success was achieved. Later, Yadav *et al*. (2010) succeeded in achieving the fertile transgenic plants (1.01%) using pCAMBIA2301 in cultivar HT-1 through the use of cotyledon explants. Yadav *et al*. (2010) observed that a total of 60% of the explants showed GUS activity; furthermore, by the addition of thiol compounds, like L-Cystine and dithiothreitol, the higher number of explants showed an increase in GUS activity. The thiol compounds are known to act as an inhibitor of antioxidants and have a wounding effect in plants (Svabova and Griga 2008). Al-Shafeay *et al*. (2011) achieved fertile transgenic plants *via Agrobacterium*-mediated transformation using pBI121 vector in cultivar Sohag1 with 1.67% frequency. Out of the various parameters tested (bacterial concentration, co-cultivation time, and explants), the co-cultivation for 1 or 2d was found better compared to longer incubation. Thereafter, Chowdhury *et al*. (2014) reported transformation efficiency of 42.66% in sesame cultivar VRI 1 using de-embryonated cotyledon explants. Chowdhury *et al*. (2014) also observed that co-cultivation of explants with *Agrobacterium* for 1 d has higher transformation efficiency compared to longer incubation with bacterial density of 1.6 OD_{600} as reported earlier by Al-Shafeay *et al*. (2011).

Along with this high concentration of BAP (30.0 µM), sucrose (9.0%) and acetosyringone helped in higher frequency of transformation in this cultivar. Gayatri and Basu (2020) reported an improved transformation protocol using *Agrobacterium* harboring pCAMBIA vector in cultivar Rama. Southern analysis revealed 1.33% transformation efficiency with low bacterial concentration ($OD_{600} < 0.6$) and for a 72-hr co-cultivation duration. The low *Agrobacterium* culture density and extended co-cultivation duration were more effective for transformation in Rama as well as other sesame cultivars (Yadav *et al*. 2010; Al-Shafeay *et al*. 2011). Overall, the transformation efficiency using *A. tumefaciencs*-mediated transformation is highly dependent on different cultivars. Therefore, as minor variations in protocols lead to variation in transformation efficiency, therefore, high scientific precision and careful handling should be followed to get the success in other sesame varieties. Chowdhury *et al*. (2017) for the first time developed the sesame transgenic lines using osmotin-like proteins and achieved both abiotic stress-tolerant and biotic stress-tolerant transgenic plants. The transgenic plants showed regulation of different biochemical parameters responsible for the regulation of combined stress (Chowdhury *et al*. 2017).

In sesame, hairy root transformation was also attempted, and some success was made by *Agrobacterium rhizogenes*-mediated system using CRISPR/Cas9. Two sesame cytochrome P450 genes responsible for sesamin and sesamolin were targeted using *A. rhizogenes*-mediated transformation, showing the feasibility of CRISPR-based genome editing in sesame (You *et al*. 2022). The particle bombardment in cultivar Rama, the genetic transformation used in apical meristematic tissue, showed approximately 16% transformation efficiency (Bhattacharyya *et al*. 2015), which is almost double the *Agrobacterium*-mediated transformation efficiency in the same cultivar (Gayatri and Basu 2020). The enhanced transformation efficiency could be due to the reduced toxicity or browning of the tissue caused by *Agrobacterium*; however, the particle bombardment method needs to be evaluated for successful transformation on other sesame varieties.

Future prospects and conclusions

In the last few decades, many efforts have been made in the area of tissue culture of the oil seed crop, sesame. The major challenges of the cultivation are yield loss due to biotic and abiotic stresses. Therefore, new research approaches are required for genetic and nutritional improvement of oil quality as well as higher yield in sesame. Although numerous regeneration protocols are reported by various researchers using different parameters and factors, but still the challenge remains because of recalcitrant nature of sesame for regeneration. It has been demonstrated that regeneration is highly genotype

Table 6. Transgenic plants of *Sesamum indicum* L. using the optimized conditions for transformation

S. No	Cultivars	Explants	Vector	basal media	Co-cultivation medium	Selection medium	Transformation frequency (%)	References
1	Özberk	Cotyledon	pBI121	MS	Semi-solid MS medium without antibiotic	BAP (8.0 mg L^{-1}) + NAA (0.1 mg L^{-1}) + kan (50.0 mg L^{-1}) + Augmentin (400.0 mg L^{-1})	No result found	Taskin *et al.*1999
2	HT -1	Cotyledon	pCAMBIA2301	MS	BAP (25 µM) + L-cysteine (400 mg L^{-1}) + dithiothreitol (1 mM)	BAP (25.0 µM) + kan (25.0 mg L^{-1}) + cefo (400.0 mg L^{-1})	1.01%	Yadav *et al.* 2010
3	Sohag 1	Cotyledon	pBI121	MS basal salt and B5 vit	BAP (2 mg L^{-1}) + IAA (1.0 mg L^{-1}) + $AgNO_3$ (5 mg L^{-1})	BAP (2.0 mg L^{-1}) + IAA (1.0 mg L^{-1}) + kan (25.0 mg L^{-1}) + cefo (200.0 mg L^{-1}) + $AgNO_3$ (5.0 mg L^{-1})	1.67%	Al-Shafeay *et al.* 2011
4	VRI-1	De-embryonated Cotyledons	pCAMBIA2301	MS	BAP (30 µM) + IAA (5.7 µM) + $AgNO_3$ (30 µM) + acetosyringone (100 µM) + 9% sucrose	BAP (30.0 µM) + IAA (5.7 µM) + ABA (4.0 µM) + kan (50.0 mg L^{-1}) + cefo (500.0 mg L^{-1}) + 3.0% sucrose + $AgNO_3$ (30.0 µM)	42.7%	Chowdhury *et al.* 2014
5	Rama	Plumule	pCAMBIA/*gfp*	MS + B5 + N6 + SH	½ MS macro + ½ B5 macro + MS micro and vit + BAP (0.25 mg L^{-1}) + acetosyringone (20 µM)	½ MS macro + ½ B5 macro + MS micro and vit + BAP (0.25 mg L^{-1}) + hygromycin (40.0 mg L^{-1}) + cefo (250.0 mg L^{-1})	9.76%	Gayatri and Basu 2020
6	TMV-7	Cotyledon	pBI121	MS	BAP (29 µM) + IAA (8 µM) + $AgNO_3$ (29 µM) + acetosyringone (20 µM)	BAP (29.0 µM) + IAA (8.0 µM) + kan (50.0 mg L^{-1}) + cefo (500.0 mg L^{-1}) + sucrose 6.0% + $AgNO_3$ (29.0 µM)	23.1%	Muthulakshmi *et al.* 2021
7	G98	Cotyledon/hairy roots	pKSE401	MS	1/10 MS + acetosyringone (20 mg L^{-1})	kan (100.0 mg L^{-1}) + timentin (200.0 mg L^{-1})	-	You *et al.* 2022

kan kanamycin, *cefo* cefotaxime

dependent. The regeneration protocols have been reported both directly and through the callus phase. It has been observed that a low salt concentration in the basal medium and a high concentration of BAP favor regeneration in this plant. The addition of $AgNO_3$ improved the regeneration frequency in some cultivars. Furthermore, it has been observed that the addition of ABA to $AgNO_3$-supplemented medium enhanced the regeneration. High sucrose pre-treatment and then sub-culturing to medium containing 3% sucrose were also found to be beneficial for shoot production. Sesame exhibits significant challenges on genetic transformation, as following co-cultivation with *Agrobacterium*, sesame often experiences a prevalent occurrence of browning and necrosis, further emphasizing its highly recalcitrant nature. The "altruistic transformation" approach was successfully used in promoting genetic transformation efficiency in different monocots and dicots using the *Wus2* and *Bbm* transcription factor in maize and sorghum (Hoerster *et al*. 2020; Nelson-Vasilchik *et al*. 2022), and *AtGRF5* and its orthologs in soybean and sunflower (Kong *et al*. 2020) can be applied for the future success of sesame transformation. Different methods, like particle gun or electroporation, should be also attempted at large in the future for the genetic transformation in this crop.

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Declarations

Compliance with ethical standards The present research does not involve human or animal participation.

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