Review Article

Factors affecting regeneration potential of tomato (*Solanum lycopersicum*) – A review

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ABSTRACT

Tomato (*Solanum lycopersicum* L.) is a major fruit crop of Solanaceae family. It is consumd worldwide and has been widely used as a model plant system for understanding biological processes, functional genomics, proteomics, and metabolomics. *In vitro* culture, a major plant biotechnology tool, exploits the totipotent nature of plant cells In recent times, genetic transformation and genome editing of plants using plant tissue and cell culture have become an important tool in both basic and applied research by insertion or deletion of target DNA. There are several factors which affect the tissue culture and regeneration of tomato. Here, we have discussed the effect of genotype; explant type, effect of age, size and orientation of explants, effect of light and temperature, nutrient media, sugar concentration, and plant growth regulators on the regeneration of tomato.

Keywords: *Agrobacterium* transformation, Genome editing, Regeneration, *Solanum lycopersicum*, Tissue culture, Tomato

INTRODUCTION

Tomato (*Solanum lycopersicum*.), belongs to the Solanaceae family, is a major horticulture crop that has attained enormous popularity in the last century. It is grown in almost every country in the world. The tomato crop is very versatile and is grown for both fresh marketing and manufacturing. Production and consumption of tomatoes have risen very rapidly in the past 25 years. Tomato is a rich source of Vitamins A and C as well as protein, and it is free of cholesterol (Hobson and Davies, 1971). Tomato contains around 20–50 mg lycopene/100 g of fruit weight (Kalloo, 1991). Lycopene is also known as carotenoids, which are natural compounds that are responsible for the color of fruit and vegetable. Lycopene is the most potent antioxidant in the carotenoid family and protects humans against free radicals that cause toxic effect on many parts of the body; it is also believed that lycopene can prevent cancer (Block *et al*., 1992; Gerster, 1997; Rao and Agarwal, 2000). Tomatoes are currently eaten at a higher rate in developed countries than in developing countries and can, therefore, be called a luxury crop.

Tomato has been widely used as a model plant system for understanding biological processes, functional genomics, proteomics, and metabolomics (Arumuganathan and Earle, 1991). The culture of plant tissue has advanced greatly since its introduction in the 1930s, when scientists began using this technique to grow cells in culture. At present it is commonly used for several different purposes such as callus induction, another culture, protoplast culture, and somatic embryogenesis.

Plant cell and tissue culture play a key role in *Agrobacterium tumefaciens* mediated genetic transformation, electroporation, particle gun, and genome editing. In recent times, genetic transformation and genome editing of plants have become an important tool in both basic and applied research by insertion or deletion of target DNA into plant genome. Transgenic and genome editing technology has progressed to extent that it is now widely used to research various biological phenomenon, namely, the effect of biochemical pathways, stress response, resistance to pathogens and more specifically, to obtain commercial crops with enhanced herbicide resistance, disease resistance, and abiotic stress tolerance (Liénard *et al*., 2007; Rai *et al*., 2013a; 2013b). *Agrobacterium*-mediated plant transformation is the most effective and low-cost system among the different plant transformation methods used for stable gene transfer. *Agrobacterium*-mediated plant transformation utilizes *A. tumefaciens* Ti plasmid to pass and incorporate a DNA fragment (T-DNA) into the host plant genome. *Agrobacterium*-mediated tomato transformation has been widely used for gene transfer, and tomato plants have been developed for a number of purposes, including enhancing biotic and abiotic stress

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tolerance (Jia *et al*., 2002), characterizing gene functions (Goel *et al*., 2010; Khare *et al*., 2010), and developing foreign proteins (Salyaev *et al*., 2007; Youm *et al*., 2008). Nevertheless, one of the major hurdles in engineering economically important tomato cultivars is the lack of a highly efficient and reproducible transformation method (Velcheva *et al*., 2005). *Agrobacterium*-mediated transformation of tomatoes was first reported in 1985 (Horsch *et al*., 1985), and since then numerous refinements have been developed by various investigators (McCormick *et al*., 1986; Hamza and Chupeau, 1993; Frary and Earle, 1996; Park *et al*., 2003; Cortina and Culianez-Macia, 2004; Velcheva *et al*., 2005; Gao *et al*., 2009; Rai *et al*., 2012). However, many of these studies do not provide crucial details of the transformation process and are limited to "model" genotypes of tomato, which makes it difficult to implement the results of other research groups to additional tomato cultivars (Sun *et al*., 2006). Researchers are actively engaged in genome editing of several crop plants. Tomato being a model crop plant has witness several genome editing researches resulting in development of many novel genome edited plants. *De novo* domestication of wild tomato using genome editing has been reported by Zsogon *et al*. (2018). They reported editing of six loci which are important for yield and productivity in present-day tomato crop lines to enable *de novo* domestication of wild *Solanum pimpinellifolium* which altered morphology of plant together with the size, number, and nutritional value of the fruits. Compared with the wild parent the genome edited *S. pimpinellifolium* lines have a threefold increase in fruit size and a tenfold increase in fruit number with altered morphology and nutritional value of the fruits.

In vitro regeneration of cultivated tomato (*S. lycopersicum*.) has been a focus of research due to the commercial importance of the crop and its suitability for further development by genetic engineering (Evans, 1989). Consequently, various studies have been carried out on the regeneration of plants from a wide variety of wild and cultivated tomato germplasm tissue and organs (Padmanabhan *et al*., 1974; Cassells, 1979; Novak and Maskova, 1979; Ancora and Ramulu, 1981; Zapata *et al*., 1981). Several *in vitro* studies on tomato have been carried out such as selection of cell lines for biotic and abiotic stresses (Stavarek and Rains, 1984; Toyoda *et al*., 1984; 1985; 1989; Rahman and Kaul, 1989); haploid growth (Gresshoff and Doy, 1972; Zagorska *et al*., 1982; 1998; Chlyah and Taarji, 1984; Shtereva *et al*., 1998); somatic hybrid production (Sink *et al*., 1986; Wijbrandi *et al*., 1988); and mass propagation (Fari *et al*., 1992). Growth of tomato has been affected by many diseases caused by bacteria, fungi, viruses, and nematodes. Bacterial wilt (*Pseudomonas solanacearum*), bacterial canker (*Corynebacterium michiganense*), and bacterial speak (*Pseudomonas syringae*) are major bacterial diseases. Common fungal diseases are fusarium wilt (*Fusarium oxysporum* f. Sp. Lycopersici), verticillium wilts (*Verticillium dahlia*), and early and late blights, caused, respectively, by *Alternaria solani* and *Phytophthora infestans*. The *Meloidogyne incognita* nematode induces an infection in the root knot. Such diseases also help to reduce the recovery of hybrid seed from field. The use of disease-resistant cultivars can be an important way to manage the aforementioned diseases. Genetic engineering techniques are playing an important role in growing disease-resistant cultivars. In 1994 Calgene, Inc. launched antisense RNA technology in tomato, which was used to improve shelf life (Flavr Savr tomato). To boost the carotenoid content and profile of tomato fruit, transgenic lines were developed by Romer *et al*. (2000), containing a bacterial carotenoid gene (crtl) encoding the phytoene desaturase enzyme, which transforms phytoene into lycopene. The existing protocols used for tomato transformation are based on shoot regeneration from leaf disc/cotyledon tissue cocultivated with disarmed *A. tumefaciens* harboring binary vector (Fillatti *et al*., 1987). In general, the efficiency of these procedures is poor (Hamza and Chapeau, 1993; Frary and Earle, 1996), as most transformed leaf/cotyledon cells do not turn into shoots (Peres *et al*., 2001). Despite several reports produced on tomato plant regeneration (Padliskikh and Yarmishin, 1990; Fari *et al*., 1992; Izadpanah and Khosh-Khui, 1992).

Apart from being a genetic engineering tool, tissue culture can be used to micropropagate high-value commercial cultivars. Developing a cost-efficient and effective protocol for the mass propagation of high-quality seedling through the cultivation of tomato tissue may help to the lower the price per seedling. A successful regeneration system of plants *in vitro* can also aid in further improving the commercially valuable cultivars for disease resistance by genetic engineering.

Vast quantities of reports on the factors affecting tissue culture of tomato are available. This information was reviewed here with view to bringing all relevant information into one forum and highlighting the areas that still need to be investigated. Hopefully this review would help many students and researchers gain a quick glimpse of the tissue culture information available in tomatoes before starting their research.

Effect of Genotype

During regeneration, most tomato genotypes respond specific to plant growth regulators (PGRs) (Kurtz and Lineberger, 1983). Variations in the quantity and form of PGRs influence both the

percentage of explants showing regeneration and the number of shoots/explant (Plastira and Perdiris, 1997). These variations are heritable and can be regulated by both cytoplasmic and nuclear genes, as shown in the reciprocal hybrids (Ohki *et al*., 1978). Genotypic variations for PGR requirements and type of explants can be seen. Frankenberger *et al*. (1981a; 1981b) demonstrated genotypic influences on regeneration. Davis *et al*., 1994, stated that the "Better Boy" cultivar regenerated only from hypocotyls, while "Spring Giant" regenerated both from hypocotyls and cotyledonary explants.

EXPLANT TYPE

Researchers used different types of explants, namely, Cotyledon, hypocotyls, pedicel, peduncle, leaf stem sections, and organogenic inflorescence. Effects of explant type (Hamza and Chupeau 1993; Park *et al*., 2003) were amply discussed. The reproductive organs in tomatoes can also be regenerated into vegetative organs. Compton and Veilleux (1991) use tomato inflorescence explants and regenerated *de novo* shoots, roots, and flowers. In addition, Applewhite *et al*., 1994, obtained explants from pedicels and peduncles of flowering tomato plants which were regenerated into roots, shoots, and ultimately whole fruit bearing plants. Duzyaman *et al*. (1994) reported that the degree of shoot regeneration was in the order of leaves ≥ cotyledons ≥ hypocotyls, and all cultivars responded similarly. Plastira and Perdikaris (1997) founded differential regeneration frequency of various explants in the order of hypocotyl > cotyledon > leaf. Hypocotyl explants also proved preferential regeneration better than cotyledon explants (Gunay and Rao, 1980). Unlike these results, Schutze and Wieczorrek (1987) reported that *in vitro* shoot regeneration from cotyledon explants was better than that of hypocotyls explants. Most of the tomato tissues tend to be highly totipotential; but choice of right explant may differ with the genotype.

EFFECT OF AGE, SIZE, AND ORIENTATION OF EXPLANTS

The success of tissue culture depends on the age of the explant. Young and soft tissue are usually more efficient for tissue culture than old and woody tissues. However, Dai *et al*. (1988) reported that the tomato's regeneration capacity increased with an increase in the explant's age. Rai *et al*. (2012) reported that cotyledon explants excised from 6 days old seedling gives higher regeneration and transformation frequency. Optimum size of explant is important for good regeneration in tomato. Very small structures as individual cells, cells clumps, and meristem are usually considered much more difficult for growth induction than entire structures such as explants of leaf, stem, or tuber. However, Schutze and Wieczorrek (1987) found that small explants produced more shoots than big explants. Chandel and Katiyar (2000) reported that the ideal size for tomato is 0.5 cm^2 for leaf explants and 1 cm long segments for shoot explants. Explants can be inoculated in polar (straight up, with the physiological base in the medium) or apolar (upside down and physiological base out of the medium) orientation on the culture medium. The polar orientation usually more easily regenerates roots and shoots than non-polar orientation. More shoots are produced from horizontally placed leaf and cotyledon explants than from vertically placed ones, and horizontally placed hypocotyls explants produce more shoots than those placed vertically straight or upside down (Duzyaman *et al*., 1994). On the other hand, Costa *et al*. (2000a) found, that the position of the cotyledon segment (apical or basal) did not lead to major variation in the average frequency of regeneration or number of shoots. Medium size explants with the right orientation may be a good option for achieving tomato shoot regeneration.

PHYSICAL FACTORS

Effect of Light and Temperature

Light is very important factor, because explants growth and differentiation depend on the duration of exposure and light quality. Light has two types of effects on regeneration:

1. The tissue culture response of tomato explant depends on the quality and amount of light used in growing the mother plant (Lercari *et al*., 2002). In general, the explants obtained from the etiolated seedling do not show strong response to regeneration (Bertram and Lercari, 2000).
2. Light condition also affects explants response at the time of incubation. Explants of tomatoes grown in white light show better regeneration than those developed in red or green light (Schutze and Wieczorrel, 1987). Pugliesi *et al*. (1999) reported that light is absolutely vital for the regeneration of tomato shoots; in the absence of light, no regeneration is possible.

Most tomato regeneration studies have used a photoperiod of 16 h. There is a lack of research about the impact of photoperiod on tomato regeneration. Cooler temperature (19°C) increased the regeneration ability of explants from tomato stem relative to warmer temperatures (28°C) (Reynolds *et al*., 1982). Conclusively, light is essential for tomato regeneration.

CHEMICAL FACTORS

Nutrient Media

MS or the modified MS medium is preferably used for tomato tissue culture (Kartha *et al*., 1976; Compton and Veilleux, 1988; 1991; Chandel and Katiyar, 2000; Park *et al*., 2001). In addition, most media contain myo-inositol at a concentration of 100 mg/L. Callus of tomato responds differently to varying concentrations of nutrients. Cano *et al*. (1990) used two modified MS (namely, NK and NB) media. In NB (MS basal mineral salt + inositol 6 mg/L + thiamine HCL 4 mg/L + nicotinic acid 0.5 mg/L + glycine 2 mg/L), fresh weight, dry weight, and callus diameter were greater than in NK (MS basal mineral salt + inositol 100 mg/L + thiamine HCL 10 mg/L + nicotinica acid 0.5 mg/L + glycine

0.5 mg/L). Selvi and Khader (1993) successfully used B5 vitamins along with major and minor nutrients of MS basal medium. Ferulic acid (0.15 mg/L), adenine (15 mg/L), and glutamine (20 mg/L) are other chemicals that have increased callus production. Chemicals such as ascorbic acid and glycine had little effect on the regeneration of the shoot (Smirnov and Smirnova, 1981). While most researchers did not observe a release of dark colored phenol during tomato organogenesis, Rao *et al*. (1985) observed an accumulation of phenolic compounds during a span of 7 days of culture. These phenolic compounds comprised 25% of the total tissue monomers found. The phenolic compound composed of vanillin (74.9%), p-coumaric acid (14.9%), p-hydroxybenzaldehyde (6.6%), and syringaldehyde (3.6%), respectively. The use of various antioxidants in tomato tissue culture has been found to inhibit the influence of phenolic compounds. Phenoxazine, alpha-tocopherol, ascorbic acid, and BHT are some antioxidants which are used in tissue culture to inhibit phenolics.

SUGAR CONCENTRATION

Only a small number of plant cell lines have been isolated which can grow autotrophically when cultivated *in vitro*. Autotrophic cells are capable of achieving self-sufficiency during photosynthesis by assimilating CO_2 in their own carbohydrates requirements (Bergmann, 1967). Usually, adding a carbon source to the growth medium is important for the cells, tissue, or organ cultures. Sucrose is used for micropropagation purposes almost universally, because it can be readily used by cells. The optimal sucrose concentration required to induce organogenesis or growth varies between genotypes. Sucrose appears to be important to the healthy growth of tomato crops and has been used by most researchers as the only source of "energy" (Compton and Veilleux, 1988; Chen *et al*., 1999; Costa *et al*., 2000a; 2000b; Venkatachalam *et al*., 2000). However, some researchers have also attempted ribose, glucose, palatinose, and furanose. The tomato callus or cell cultures cultured on ribose-media as the sole source of carbon, the tissues turned dark brown, and ceased to grow. However, bright green tissues emerged from about 3% of the brown necrotic callus tissue after around 60 days (Locy *et al*., 1995). Furthermore, successful tomato hypocotyl cultures have been developed on a medium containing 2% glucose (Zelcer *et al*., 1984). Sucrose at concentration of 30 g/L (compared to 5, 10, or 20 g/L) was considered optimal for the growth of tomato microplants (Schnapp and Preece, 1986). This concentration of sucrose has been used by most researchers in their media of initiation and multiplication (Compton and Veilleux, 1988; Chen *et al*., 1999; Costa *et al*., 2000a; 2000b; Venkatachalam *et al*., 2000, Rai *et al*., 2012).

PGRs

PGRs are small organic molecules formed in specific tissues or organs. It is known that crop cultivation *in vitro* is impossible without PGRs (George, 1996). PGRs influence morphogenic response by altering specific physiological processes. For example, cytokinin and auxin treatment influence the accumulation of starch and the protein electrophoretic pattern in tomato cultures (Branca *et al*., 1994). A wide range of PGRs at different concentrations have been used for tomato regeneration. The concentration of the growth regulators used depends on the cultivar being cultured and the use of the specific cytokinin or auxin. The change in exposure period results in difference in the time needed for organogenesis and in the number of shoots developed on an explant (Padmanabhan *et al*., 1974; Cassells, 1979; Novak and Maskova, 1979; Ancora and Ramulu, 1981; Zapata *et al*., 1981; Chen *et al*., 1999; Costa *et al*., 2000a, 2000b; Venkatachalam *et al*., 2000). Plantlets are usually regenerated either directly (Dwivedi *et al*., 1990), or from the primary callus (Jawahar *et al*., 1997). Subculture of unorganized callus to a medium in which the cytokinin to auxins ratio is increased, or in which only cytokinin is present, leads to differentiation of the shoot (Gresshoff and Doy, 1972).

There are four main cytokinins, namely, zeatin, 2-iP, BA, and kinetin. They can be used for organogenesis in tomato either separately or together with auxins. Haploid shoots can be regenerated from the anther callus by transferring the callus from the high auxin (5.0 mg/L NAA) and low cytokinin (0.01 mg/L kin) medium to another medium containing low auxin and high cytokinin (0.1 mg/L NAA and 2.0 mg/L kin). Long-term callus cultivation was accomplished on a medium with low NAA concentrations of 1.0 mg/L (Imanishi *et al*., 1976). Vnuchkova (1977a; 1977b) analyzed 150 different media and concluded that kinetin and IAA combinations (6.0 mg^{-1} IAA and 5.0 mg/L kinetin or 5.0 mg/L IAA and 8.0 mg/L kinetin) are the most suitable for the formation of meristem in tomato explants. Gunay and Rao (1980) found that an IAA-BA combination for shoot regeneration was superior to the IAA-kinetin. Kartha *et al*. (1976) reported that BA or zeatin alone induced shoot formation from leaf callus. Zeatin and BA were also found superior to kinetin for tomato leaf explants to form shoots (Dhruva *et al*., 1978). Rai *et al*. (2012) reported that the highest regeneration and transformation frequency (30.89%) were found on MS medium supplemented with 9.3 µM Kin, 8.9 µM BA, and 0.4 mg/L thiamine. Cassells (1979) reported that stem explants of tomato cv. Craigella cultured on a medium containing cytokinin produced adventitious shoots at the top of the explant. However, addition of the auxin-transport inhibitor TIBA stimulated caulogenesis with loss of polarity.

CONCLUSION AND FUTURE PROSPECTS

Tissue culture techniques are progressing rapidly in tomatoes. There is, however, still a long way to go before hybrid cultivars can be raised economically feasible through tissue culture. It is because of the unique genotypical necessity of PGRs and the availability of 100s of hybrid tomato cultivars. Various researchers used a wide variety of PGRs at varying concentrations for various tomato cultivars. Furthermore, various types of explants have also been used and the option of the correct explant is often based on genotypes. The literature fails to address many other difficulties faced during culture. The

latest literature on tomato organogenesis and micropropagation primarily discusses optimization of PGR type and concentration and explant type selection. The development of protocols for morphogenesis of commercially important cultivars involves an enhanced understanding of various physical and chemical factors. Techniques such as regeneration and somatic embryogenesis are necessary for the development of genetically engineered as well as genome edited plants from cells. Such techniques are also required to produce a great number of elite transgenic plants. There are numerous studies on tomato genetic instability under *in vitro* conditions, thus requiring evaluation of somaclonal variations resulting from tissue culture.

Due to the current anti-GMO consumer mindset, a wise combination of plant breeding, molecular biology, and tissue culture techniques should be introduced to exploit these fields for both the production and multiplication of new cultivars. Somaclonal variations arising from tissue culture can also be used to assist with tomato breeding.

There is enough potential in tissue culture techniques for the genetic improvement as well as tomato micropropagation. This ability can only be realized if unique cultivar specific morphogenesis protocols are developed.

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