



Biology and biotechnological aspect of sweet potato (*Ipomoea batatas* L.): a commercially important tuber crop

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Abstract

Main conclusion This review highlights the economic importance of sweet potato and discusses new varieties, agronomic and cultivation practices, pest and disease control efforts, plant tissue culture protocols, and unexplored research areas involving this plant.

Abstract Sweet potato is widely consumed in many countries around the world, including India, South Africa and China. Due to its valuable nutritional composition and highly beneficial bioactive compounds, sweet potato is considered a major tuber crop in India. Based on the volume of production, this plant ranks seventh in the world among all food crops. Sweet potato is considered a “Superfood” by the ‘Centre for Science in the Public Interest’ (CSPI), USA. This plant is mostly propagated through vegetative propagation using vine cuttings or tubers. However, this process is costly, labour-intensive, and comparatively slow. Conventional propagation methods are not able to supply sufficient disease-free planting materials to farmers to sustain steady tuber production. Therefore, there is an urgent need to use various biotechnological approaches, such as cell, tissue, and organ culture, for the large-scale production of healthy and disease-free planting material for commercial purposes throughout the year. In the last five decades, a number of tissue culture protocols have been developed for the production of in vitro plants through meristem culture, direct adventitious organogenesis, callus culture and somatic embryogenesis. Moreover, little research has been done on synthetic seed technology for the in vitro conservation and propagation of sweet potato. The current review comprehensively describes the biology, i.e., plant phenotypic description, vegetative growth, agronomy and cultivation, pests and diseases, varieties, and conventional methods of propagation, as well as biotechnological implementation, of this tuber crop. Furthermore, the explored and unexplored areas of research in sweet potato using biotechnological approaches have been reviewed.

Keywords Agronomy · Pest and diseases · Propagation · Sweet potato · Tissue culture · Varieties

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Introduction

Ipomoea batatas (L.) Lam, more commonly known as sweet potato, is a dicotyledonous and perennial tuber crop belonging to the family Convolvulaceae. Sweet potato is well known for its food, medicinal and industrial value (Chee et al. 1992; Ayeleso et al. 2016; Tadda et al. 2022). It is used in traditional systems of medicine for the treatment of various diseases, such as type 2 diabetes, oral infection, anaemia, hypertension, prostatitis, tumours, stomach cancer, cardiovascular disease, allergies, ageing, dysentery, constipation, eye diseases, arthritis, rheumatism, fever, dengue, nausea, and splenosis. (Ludvik

et al. 2004; Abel and Busia 2005; Islam 2006; Emmanuel 2010; Pochapski et al. 2011a, b; Mohanraj and Sivasankar 2014; Milind and Monika 2015). In addition, the leaves of the plants have the potential to fight against age-related macular degeneration (AMD) (Khachatryan et al. 2003; Abidin et al. 2017). Studies have revealed that the plant also possesses several pharmaceutical properties, such as antimicrobial, antioxidant, anticancer, anticoagulant, anti-inflammatory, and antiulcer activities (Meira et al. 2012; Hermes et al. 2013; Mohanraj and Sivasankar 2014).

Sweet potato is usually consumed as a staple food after rice and wheat in many countries around the world, including South Africa and China (Milind and Monika 2015; Akomeah et al. 2019; Tadda et al. 2022), and it is recognized as a major tuber crop (Ghasemzadeh et al. 2016) due to its nutritional components and health-promoting phytochemicals (Cho et al. 2003; Teow et al. 2007; Chauhan et al. 2021), such as starch, protein, vitamins, minerals, carotenoids, anthocyanins, caffeoylquinic acid, and polyphenols. (Ayeleso et al. 2016; Tanaka et al. 2017). This plant is the seventh in the world among all food crops based on production, and the Centre for Science in the Public Interest (CSPI) in the USA designated it a “Superfood” that can enhance human health (Kang et al. 2017). The tubers are used as a raw vegetable for the preparation of curries, mixtures, chips, breads, buns, cakes, biscuits, fish pasties, chapatti, jam, ketchup, juices and other value-added products (Owori et al. 2007; Abidin et al. 2015). However, the leaves are often used as green leafy vegetables, as they have more polyphenols than other commercial green leafy vegetables (Islam et al. 2003; Owori et al. 2007). The starchy tuber of sweet potato is calorie-rich and has been used as a subsidiary food, livestock feed and raw material in industries producing starch, liquid glucose, citric acid, monosodium glutamate, and ethanol in different countries (Magoon et al. 1970; Nedunchezhiyan et al. 2012; Jena and Kar 2019). The Food and Agriculture Organisation (FAO) has reported that sweet potato leaves and shoots are good sources of vitamins A, B, and C, as well as lutein. Due to its rich nutritional content as well as wide adaptability to marginal land (from tropical to temperate zones), sweet potato has a high potential for the prevention of malnutrition and the ability to increase food security in developing countries (Kang et al. 2017; Akomeah et al. 2019). In this review, contemporary information on the biology of sweet potato, such as plant phenotypic description, vegetative growth, agronomy and cultivation, pests and diseases, varieties, and conventional methods of propagation, as well as studies related to biotechnological advances, such as meristem culture, callus culture, direct adventitious organogenesis, somatic embryogenesis, synthetic seed technology, biochemical

analysis and genetic fidelity, and the genetic transformation of sweet potato are discussed.

Plant phenotypic description

Sweet potato is a perennial herb with swollen roots called tubers or storage roots; its sap is milky in colour, and the axial parts are glabrous or pilose. The stems are ascending, rarely twining, green or purplish, highly branched, and rooting at the nodes. The petiole size is approximately 2.5–20 cm; the leaf blade is broadly ovate to circular, 4–13 × 3–13 cm, with its margin entire or palmately 3–7 lobed. Lobes are broadly ovate to linear-lanceolate, sparsely pilose or glabrous. The inflorescences of sweet potato have 3 to 7 flowers; the peduncle 2 to 10.5 cm long, stout, and angular; and the bracts are early deciduous with a lanceolate size of 2 to 4 mm. The pedicel size is 2 to 10 mm. The sepals are oblong or elliptical, unequal, glabrous or pilose abaxially, with a margin that is ciliate, apex acute, and mucronulate; the outer 2 sepals and inner 3 sepals have diameters of 7 to 10 mm and 8 to 11 mm, respectively. The corolla may be pink or white or pale purple to purple in colour with a darker centre and be campanulate to funnel form, 3 to 4 cm long, and glabrous. The capsule is rarely produced, ovoid or depressed globose. The seed is glabrous (Saxena 1986).

Vegetative growth

Sweet potato is a branched creeping vine with spirally arranged heart-shaped leaves. Flowers are white or lavender in colour. The swollen root, i.e., the tuber of the plant plays a key role in storing nutrients for the growth and development of the plant. The tuber has various shapes, including ellipsoid, fusiform, or elongated shapes, and colours, such as red, yellow, brown, white, and purple. Sweet potato stems can grow up to 4 m (approximately 13 ft) in length. The plant is generally cultivated as an annual crop and harvested after one growing season.

Agronomy and cultivation practices

Sweet potato requires well-drained loam and clay loam soils for better growth. However, sandy loam with clay subsoil is also ideal for the cultivation of this plant. In sandy soil, sweet potato roots easily penetrate the soil and grow properly, while heavy clayey and compact soil restricts the growth of its roots (Nedunchezhiyan and Ray 2010). The growth of sweet potatoes is also influenced by the pH of the soil. A soil pH of 5.5 to 6.5 is optimum for the cultivation of sweet potatoes. Increasing or decreasing the pH of soil obstructs the growth of sweet potato by causing pox and scurf diseases or aluminium toxicity, respectively (Mukherjee et al. 2006; Nedunchezhiyan and Ray 2010;

Nedunchezhiyan et al. 2012). This plant requires moderate temperature (21–26 °C) but abundant sunshine. The plant is able to tolerate drought conditions, but it cannot grow in water logging conditions. More details about the agronomic conditions, field preparation, and cultivation practices have been reviewed earlier by Nedunchezhiyan et al. (2012).

Pests and diseases

Various pests and diseases are widely recorded in sweet potato. The tubers and vines are commonly attacked by different disease-causing pathogens such as nematodes and insects, which adversely affect the yield and quality of tubers (Nedunchezhiyan et al. 2012). *Meloidogyne* spp. and *Rotylenchulus reniformis* are the commonly known nematode pests of sweet potato in the tropics (Mohandas 2006). *Cylas formicarius* is claimed to be a major sweet potato weevil pest in developing countries; its larvae and adults feed on the roots and cause damage both in the field and during storage in different regions of the world (Ray and Ravi 2005). *Eusepeus postfasciatus* is considered a serious insect pest in South America, the Caribbean and the Pacific (Yasuda 1998), while *Omphisa anastomosalis* is reported as a sweet potato vine borer in India, Malaysia, and China (Rajamma and Premkumar 1994). Similarly, fungal and viral diseases of sweet potato have also been observed under field conditions. *Fusarium oxysporum* Schlect. F. sp. *Batatas*, a destructive pathogen in the United States, is a fungus that causes stem rot disease in sweet potato (Woolfe, 1992). Sweet potato leaves or roots are also vulnerable to several viruses, including *Sweet Potato Feathery Mottle Virus* (SPFMV) (Nedunchezhiyan et al. 2012).

Varieties of sweet potato

There has been increasing interest in sweet potato breeding globally. As a result, hundreds of sweet potato varieties have been developed considering the importance of the crop in securing the livelihood and income generation of associated industries. The names of sweet potato varieties developed in different countries have been described in detail earlier by Nendunchezhiyan et al. (2012). The Indian Council of Agricultural Research-Central Tuber Crops Research Institute (ICAR-CTCRI) and different All India Coordinated Research Project (AICRP) centres have released approximately 40 varieties of sweet potatoes alone. All the varieties were released for cultivation in Kerala, Andhra Pradesh, Maharashtra, Odisha, Jharkhand, Chattishgarh, Bihar, Assam, West Bengal, Karnataka, Tamilnadu, and Northeastern regions of India (Nendunchezhiyan et al. 2012; Sunitha et al. 2018, Pati et al. 2021). All 40 varieties were divided into three categories based on flesh colour: orange, purple, and white-fleshed sweet potato (Fig. 1 A-C).

Out of these 40 varieties, six varieties, ‘Bhu Sona’, ‘Bhu Kanti’, ‘Bhu Ja’, ‘Gouri’, ‘Kamala Sundari’, and ‘Co-5’, are rich in β -carotene content, and the highest β -carotene content was recorded in the variety ‘Bhu Sona’ (Fig. 1 A; 14.0 mg/100 g). These varieties have orange flesh and are known for their nutritional value, yield, use as colouring agents, and field tolerance to mid-season drought and salinity stress (Pati et al. 2021). Orange-fleshed sweet potato varieties contain β -carotene, which is a precursor of vitamin A. Thus, these varieties can be promoted as food for children in areas where night blindness is a problem due to malnutrition. ICAR-CTCRI, Regional Centre, Bhubaneswar, has released the anthocyanin-rich (85–90 mg/100 g) sweet potato variety ‘Bhu Krishna’ (Fig. 1 B), which has purple flesh and the ability to grow under medium stress and salinity stress conditions. Anthocyanins are naturally soluble pigments with a variety of medicinal and pharmaceutical properties (Cho et al. 2003; Fan et al. 2008; Nendunchezhiyan et al. 2012). The white-fleshed variety ‘Kishan’ is the most popular sweet potato in Odisha based on farmer choice due to its high yield and drought tolerance ability (Fig. 1 C). Its average tuber yield is 17–18 tonnes/hectare, with a dry matter of 32–34%, starch of 29–30% and total sugar of 3–3.5% (CTCRI 2014).

Conventional methods of propagation

Sweet potato is a perennial tuber crop plant that is normally cultivated as an annual crop plant. The plant is traditionally propagated by vegetative propagation using vine/stem cuttings and tubers (Akomeah et al. 2019). The sprouts produced from the tuber are excellent planting material for the vegetative propagation of sweet potato (Khan and Doty 2009). The production of planting materials through tubers is more cost-effective than that through vine/stem cuttings. As far as stem cutting is concerned, the apical and middle parts of the stem have been found to be the best sources for obtaining higher tuber yield (Mukhopadhyay et al. 1990; Nedunchezhiyan et al. 2012). The basal end of the stem is difficult to establish as a plant because it is thick and woody and has a greater chance of weevil attack (Nair 2006). The production rate of the tuber also depends on the length of the stem used for propagation (Nedunchezhiyan et al. 2012). However, there are certain limitations in the conventional method of propagation using stem/vine cuttings or tubers, i.e., it is slow, time-consuming, and season dependent. These parts of the plants are also attacked by various pathogens, including nematodes and insect pests (Nedunchezhiyan et al. 2012). *Meloidogyne* spp. and *Rotylenchulus reniformis* are two well-known nematode pests of sweet potato; they directly attach to the fibres and fleshy roots and reduce the yield and quality of the tuber (Mohandas 2006). In addition, as sweet potato is predominantly a vegetatively propagated crop, pathogens usually accumulate in its vegetative

Fig. 1 Different varieties of sweet potato: **A** Bhu Sona (Orange-fleshed sweet potato); **B** Bhu Krishan (Purple-fleshed sweet potato); **C** Kishan (White-fleshed sweet potato)



propagules, such as vine/stem cuttings and tubers. They also spread from one generation to the next, causing great losses in yield and the production of poor-quality tubers (Akomeah et al. 2019; Tadda et al. 2022). Thus, the conventional method of propagation is not always adequate for the production of large-scale, uniform, disease-free planting materials throughout the year to fulfil the demand of farmers for the sustained steady production of tubers (Tadda et al. 2022). Biotechnological approaches using different plant tissue culture techniques can circumvent these problems by producing a large number of true-to-type plants in different species and are already evident.

Biotechnological advances through plant tissue culture in sweet potato

Plant tissue culture is an efficient and reliable method for the large-scale production of high-quality and disease-free plants in a short time period within a small space and can supply elite planting materials to farmers throughout the year (Butt et al. 2015; Mukhopadhyay et al. 2016; Akomeah

et al. 2019; Behera et al. 2019, 2022; Tadda et al. 2022). Additionally, this technique can be used to produce genetically improved plants with disease resistance or abiotic stress resistance that can aid in the propagation of sweet potato. Biotechnological advances through plant tissue culture also have the potential to provide new prospects for the improvement of sweet potato with high nutritional and pharmaceutical value. To date, several works have been published on the development of an *in vitro* plant regeneration protocol for sweet potato through meristem culture, callus culture, direct adventitious organogenesis, somatic embryogenesis, and synthetic seed technology. In this section, we emphasize the research progress made in sweet potato based on various aspects of tissue culture and propose unexplored areas that might be considered for future research (Fig. 2).

Multiple shoot proliferation via meristem culture

There are several factors, including the genotype and physiological condition of the donor plant, type of explant, nutrient medium, carbon source, plant growth regulators, and

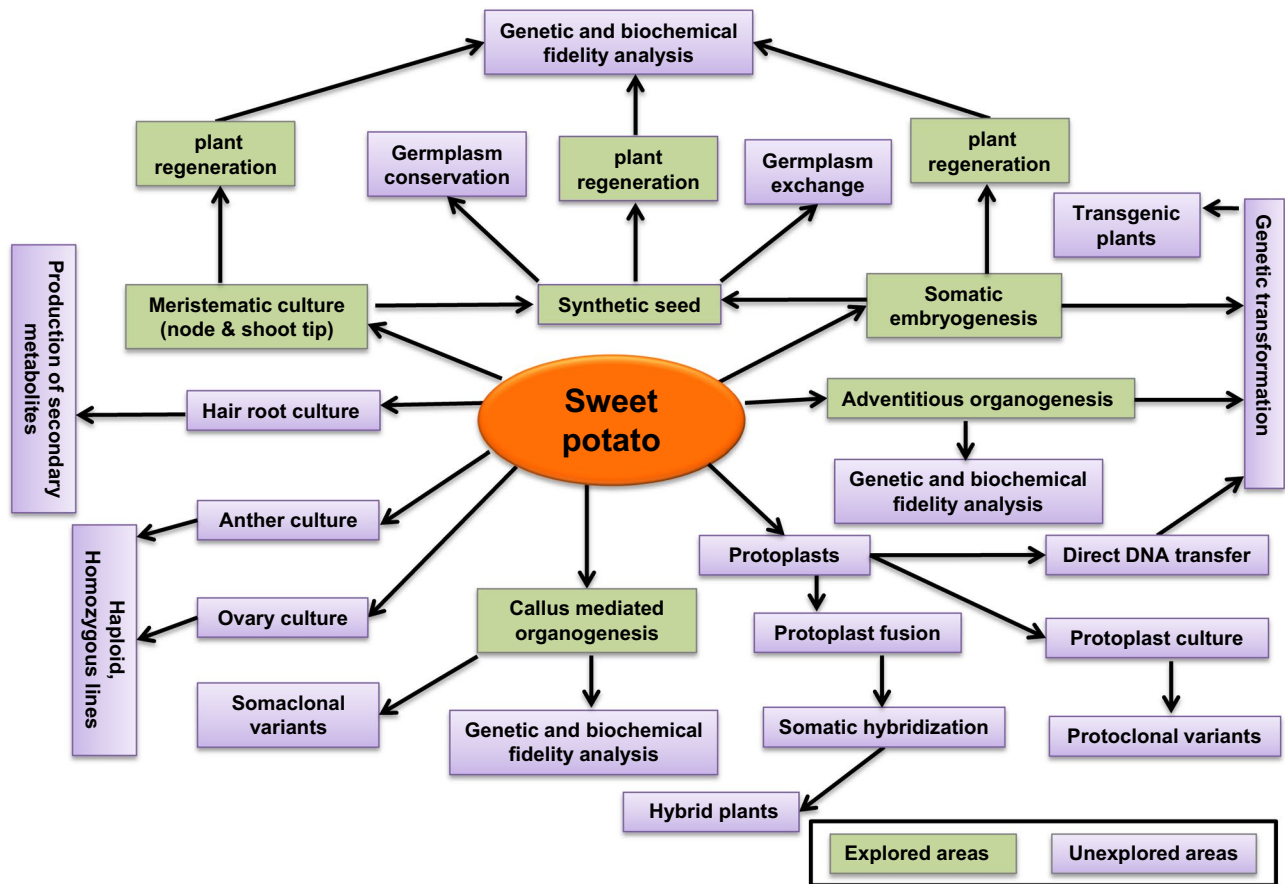


Fig. 2 Biotechnological intervention through plant tissue culture in sweet potato: explored areas and unexplored areas

additives, that play a pivotal role in multiple shoot proliferation by meristem culture. The successful development of a micropropagation protocol depends on the selection of plant parts as the starting material or explant. To date, several types of explants, including nodal segments, vines, axillary buds, shoot tips, apical buds, and lateral buds, from mature and in vitro plants have been used as explants for multiple shoot proliferation through meristem culture of sweet potato. However, nodal segments or nodes have been recognized as the best or most commonly used explant for multiple shoot proliferation of sweet potato (Table 1). Generally, nodal explants were more responsive to shoot proliferation than other explants of sweet potato, which may be due to the presence of active meristematic tissues (Addae-Frimpomaah 2014; Ndagijimana et al. 2014; Alula et al. 2018). The nutrient medium plays a critical role in bud break and shoot proliferation in the apical or axillary meristem of mature sweet potato plants, as documented in Table 1. Different types of nutrient media, such as full-strength Murashige and Skoog’s (MS) (1962) basal medium, half-strength MS (½ MS) medium, modified MS medium (MMS), and Linsmaier and Skoog (LS) (1965) medium, have been used by various researchers for the micropropagation of sweet potato.

However, MS basal medium was found to be the most suitable medium for shoot initiation, multiplication and elongation and rooting in sweet potato (Table 1). Owori et al. (2007) used a vegetative fertilizer called Easygro as a basal medium instead of MS medium (Table 1). In addition, the inclusion of a carbon source is also necessary for the growth and development of in vitro cultured shoots of plants such as sweet potato. The carbon source is supplied as a different form of sugar, such as sucrose, glucose, maltose, fructose, sorbitol, dextrose, and table sugar, and is available commercially for plant tissue culture (Kadota and Niimi 2004; Kaur et al. 2022). Carbon sources serve as an energy source and hold osmotic stability between both the cell and the external environment in the culture medium (Kaur et al. 2022). In the case of sweet potato, sucrose (30 g/l) was found to be a suitable carbon source for in vitro shoot proliferation via meristems (Kuo et al. 1985; Mengs et al. 2018; Arif and Bahari 2019). However, table sugar (30 g/l) was used as a cost-effective carbon source in a meristem culture study in sweet potato by Oggero et al. (2011; 2012).

A nutrient medium without any plant growth regulators or additives is not suitable for multiple shoot regeneration. In sweet potato, basal culture medium supplemented with

Table 1 In vitro plant regeneration through meristematic organogenesis of sweet potato

Clone/cultivar/variety	Explant	Results	MS basal medium with plant growth regulators		References
			Shooting	Rooting	
<i>Ipomoea batatas</i> L. cv. Owarika Red, 907, 888	Apical bud	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + NAA (1.0 mg/l) + GA ₃ (10.0 mg/l)		Elliott 1969
<i>Ipomoea batatas</i> L. cv. Jewel	Axillary buds	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + KIN (0.5 mg/l) + IAA (0.2 mg/l)		Alconero et al. 1975
<i>Ipomoea batatas</i> L. cv. White Start, PI315343	Vines	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + BA (1.0 mg/l) + KIN (1.0 mg/l) + IAA (1.0 mg/l)		Liz and Conover 1978
<i>Ipomoea batatas</i> L	Tubers	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + BA (5.0 mg/l) + IAA (1.2 mg/l)		Liao and Chung 1979
<i>Ipomoea batatas</i> L	Apical bud from tuber	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + BA (0.5 mg/l) + IAA (0.2 mg/l)		Frison and Ng 1981
<i>Ipomoea batatas</i> L. cv. AIS 0122-2, CN 1108-13	Apical bud from tuber	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + BA (1.0 mg/l) + IAA (1.0 mg/l)		Kuo et al. 1985
<i>Ipomoea batatas</i> L	Apical meristem	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + KIN (1.0 mg/l) + NAA (0.1 mg/l) + GA ₃ (1.0 mg/l)		Rey and Myoginski 1985
<i>Ipomoea batatas</i> L	Nodal segment		MS medium + GA ₃ (20 mg/l) + L-arginine (100 mg/l) + Ascorbic acid (200 mg/l) + Putrescence (20 mg/l)		Dodds et al. 1991
<i>Ipomoea batatas</i> L. cv. Georgia Red	Meristem tips	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + KIN (2.5–5.0 mg/l)		Macro and Walkey 1992
<i>Ipomoea batatas</i> L	Vines or tuber	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + BA (0.5 mg/l) + IBA (0.1 mg/l)		Beetham and Mason 1992
<i>Ipomoea batatas</i> L. cv. UPL-SP	Axillary bud	Simultaneously shooting and rooting, plantlet regeneration	MS medium + KIN (1.0 mg/l) + GA ₃ (1.0 mg/l)		Zamora and Gruezo 1993
<i>Ipomoea batatas</i> L. cv. Jewel	Stem	Plantlets	MS medium + IAA (0.5 mg/l)	NI	Gonzalez et al. 1992
<i>Ipomoea batatas</i> L. cv. 8570	Node	Shoot proliferation	MS medium + BA (1.0 mg/l) + NAA (1.0 mg/l) + NAA (0.5 mg/l) + GA ₃ (0.05 mg/l) + NaCl (2.0 mg/l)		Mukherjee 2002
<i>Ipomoea batatas</i> L cv. Gaozi No. 1	Node	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + NAA (1.0 mg/l)		Gong et al. 2005
<i>Ipomoea batatas</i> L. cv. Mozambique White	Node	Plantlets	MS medium		Matimati et al. 2005

Table 1 (continued)

Clone/cultivar/variety	Explant	Results	MS basal medium with plant growth regulators		References
			Shooting	Rooting	
<i>Ipomoea batatas</i> L. cv. Purple Sweet potato	Shoot tip	Shoot proliferation, rooting, and plantlet formation	MS medium + BA (1.0 mg/l)	MS medium + BA (0.5 mg/l) + NAA (0.2 mg/l)	Yang 2010
<i>Ipomoea batatas</i> L. var. Awassa-83	Node	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (2.0 mg/l)	½ MS medium + IBA (0.1 mg/l)	Dugassa and Feyissa 2011
<i>Ipomoea batatas</i> L. var. Awassa local	Node	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (2.0 mg/l)	½ MS medium + IBA (0.1 mg/l)	Dugassa and Feyissa 2011
<i>Ipomoea batatas</i> L. var. Guntute	Node	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (3.0 mg/l)	½ MS medium	Dugassa and Feyissa 2011
<i>Ipomoea batatas</i> L. var. KEMB 36	Vine	Shoot proliferation, rooting, and plantlet formation	Modified MS medium + Table sugar (3.0%) gelled with 0.3% gelrite	MS medium + Table sugar (30 g/l) gelled with 3.0 g/l	Oggero et al. 2011
<i>Ipomoea batatas</i> L. cv. Tainurey	Node	Plantlet	Easygro (vegetative fertilizer) + Table sugar (30 g/l) + Agar (9 g/l)		Oggero et al. 2012
<i>Ipomoea batatas</i> L.	Node	Plantlet	MS medium + NAA (2.0 mg/l) + Sucrose (20 g/l)		Ozturk et al. 2012
<i>Ipomoea batatas</i> L. cv. Carmen Rubin	Node	Plantlet	MS medium + KIN (0.1 mg/l) + GA ₃ (1.0 mg/l)		Dolinski and Olek 2013
<i>Ipomoea batatas</i> L.	Node	Plantlet	MS medium		Ubalua and Okoroafor 2013
<i>Ipomoea batatas</i> L. cv. UE007	Node	Plantlet	MS medium + BA (2.0 mg/l)		Addae-Frimpomaah 2014
<i>Ipomoea batatas</i> L. cv. Gihinga-mukungu	Node	Simultaneously shooting and rooting, plantlet regeneration	MS medium + GA ₃ (20.0 µM)		Ndagijimana et al. 2014
<i>Ipomoea batatas</i> L. cv. Ukerewe	Node	Simultaneously shooting and rooting, plantlet regeneration	MS medium + Sucrose (150 mM)		Ndagijimana et al. 2014
<i>Ipomoea batatas</i> L. cv. Brondal	Meristem tip	Plantlets	MS medium + BA (1.0 mg/l) + GA ₃ (10 mg/l)		Masekesa et al. 2016
<i>Ipomoea batatas</i> L. cv. UENF 1931	Node	Plantlet	MS medium + Sucrose (2.0%)		Vettorazzi et al. 2017
<i>Ipomoea batatas</i> L. var. Beletech	Apical meristem	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (0.75 mg/l) + KIN (0.5 mg/l)	MS medium + IBA (1.0 mg/l) + NAA (0.5 mg/l)	Alula et al. 2018
<i>Ipomoea batatas</i> L. cv. King J	Axillary bud	Simultaneously shoot proliferation and rooting, plantlet regeneration	MS medium + BA (0.5 mg/l) + NAA (0.05 mg/l) + GA ₃ (0.5 mg/l)		Abubakar et al. 2018
<i>Ipomoea batatas</i> L. cv. Amitchewin (yellow flesh sweet potato)	Nodal explant	Shoot proliferation and rooting, plantlet regeneration	MS medium + BA (1.0 mg/l) + NAA (0.1 mg/l) + Sucrose (30 g/l)	½ MS medium	Dousoh et al. 2018a
<i>Ipomoea batatas</i> L. var. Kullufo	Lateral bud	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (0.5 mg/l)	MS medium + IBA (0.5 mg/l)	Mengs et al. 2018
<i>Ipomoea batatas</i> L. var. Tulla	Lateral bud	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (0.5 mg/l)	MS medium + IBA (0.25 mg/l)	Mengs et al. 2018
<i>Ipomoea batatas</i> L. cv. Purple flesh sweet potato	In vitro shoot	Shoot proliferation	½ MS medium + BA (3.0 mg/l) + NAA (1.0 mg/l)	NI	Arif and Bahari 2019

Table 1 (continued)

Clone/cultivar/variety	Explant	Results	MS basal medium with plant growth regulators		References
			Shooting	Rooting	
<i>Ipomoea batatas</i> L. var. Gouri	Nodal explant	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (1.0 mg/l) + GA ₃ (1.0 mg/l) + Sucrose (30 g/l)	MS medium + IBA (0.5 mg/l) + Sucrose (30 g/l)	Shajji et al. 2019
<i>Ipomoea batatas</i> L.	Shoot tip	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (1.0 mg/l) + Sucrose (30 g/l)	½ MS medium	Beyene et al. 2019
<i>Ipomoea batatas</i> L. Var. orange flesh sweet potato	Shoot tip	Shoot proliferation, rooting, and plantlet regeneration	MS medium + BA (1.0 mg/l) + Sucrose (30 g/l)	½ MS medium + IBA (0.5 mg/l)	Beyene et al. 2020
<i>Ipomoea batatas</i> L. (red-peeled sweet potato)	Nodal explant	Shoot proliferation, rooting, and plantlet regeneration	½ MS medium + BA (2.0 mg/l) + Oxalic acid (100 mg/l) + Sucrose (30 g/l) ↓ ½ MS medium	½ MS medium	Dewir et al. 2020
<i>Ipomoea batatas</i> L.	Nodal explant	Shoot proliferation, rooting, and plantlet regeneration	LS medium + KIN (0.1 mg/l) + GA ₃ (1.0 mg/l)	LS medium + IAA (0.5 mg/l)	Karan and Ozdemir 2021

½ MS half strength Murashige and Skoog (1962) medium, BA- N⁶ benzyladenine, GA₃ gibberellic acid, IAA indole-3-acetic acid, IBA indole-3-butyric acid, KIN kinetin, MS Murashige and Skoog (1962) medium, NAA naphthaleneacetic acid, NaCl sodium chloride, NI no information, LS Linsmaier and Skoog (1965) medium

different types and concentrations of cytokinins, such as N⁶-benzyladenine (BA) and kinetin (KIN), either alone or in combination with different types of auxins, such as α-naphthaleneacetic acid (NAA), indole-3-butyric acid (IBA), and indole-3-acetic acid (IAA), has been used for multiple shoot initiation, proliferation and elongation or plantlet regeneration (Table 1). MS medium supplemented with BA has been frequently used by several researchers for the multiplication of shoots in sweet potato (Yang 2010; Dugassa and Feyissa 2011; Addae-Frimpomaah 2014; Beyene et al. 2019, 2020). BA was also reported to be the most effective cytokinin in multiple shoot formation due to the stability of ribosides and nucleotides (Behera et al., 2015). In comparison to other cytokinins, BA produced the maximum number of in vitro regenerated shoots or plantlets in sweet potato, which may be due to the aforementioned stability. When BA was combined with KIN, IAA, IBA, or NAA in the culture medium, it had a synergistic effect on multiple shoot proliferation or plantlet regeneration in sweet potato (Table 1). Several researchers reported simultaneously multiple shoot and root formation from a single explant in the same multiplication medium (Mesekeza et al. 2016; Vettorazzi et al. 2017; Abubakar et al. 2018).

Direct adventitious shoot organogenesis

In direct adventitious shoot organogenesis, the plant regenerates from a non-meristematic explant without the formation of a callus. Plants obtained through adventitious organogenesis directly from explants are usually genetically stable (Naik and Chand 2011). To date, direct adventitious shoot organogenesis in sweet potato has rarely been reported. Dessai et al. (1995) reported adventitious shoot organogenesis using leaf explants of twenty-seven different genotypes of sweet potato. All of the leaf explants were inoculated on MS medium supplemented with different concentrations (0.2–1.0 mg/l) of 2,4-dichlorophenoxyacetic acid (2,4-D) for 3 days, followed by transfer to 0.2 mg/l Zeatin riboside (ZR)-supplemented medium for shoot multiplication. The maximum percentage of explants from the PI 318,446–3 genotype were generated by multiple shoot formation on MS medium supplemented with 0.2 mg/l 2,4-D. However, Gosukonda et al. (1995) reported the direct adventitious shoot organogenesis of 13 different genotypes of sweet potato using petiole as the explant. Petiole explants were inoculated on MS medium supplemented with 0.2 mg/l 2,4-D for 3 days and then transferred to MS medium supplemented with 0.05 mg/l Thidiazuron (TDZ) and 0.05 mg/l N⁶-2-isopentenyl adenine (2iP) for shoot organogenesis. Most genotypes responded to direct adventitious shoot organogenesis on this medium. The position of the explant (petiole) on the medium has also been shown to influence shoot proliferation (Gosukonda et al., 1995). Furthermore, adventitious shoot organogenesis of sweet potato using root explants was

reported by Delgado-Paredes et al. (2017). The root explants were inoculated on liquid MS medium supplemented with 2.0 mg/l BA and incubated for 2 months for complete plantlet formation. Recently, Masekesa et al. (2021) reported that MS medium supplemented with 0.05 mg/l 2,4-D and 0.5 mg/l KIN was the best for direct adventitious shoot organogenesis from leaf explants of the sweet potato cv. Brondal. These *in vitro* regenerated shoots were successfully rooted on a growth regulator-free MS medium.

Callus-mediated organogenesis

Callus-mediated shoot organogenesis is an important pathway in tissue culture techniques that helps to produce a large number of plants. To date, very few reports are available on callus-mediated shoot organogenesis of sweet potato. Various types of explants, such as leaf lamina, internodes, petioles, and lateral buds, and MS media supplemented with different concentrations and combinations of growth regulators, such as 2,4-D, BA, NAA, and KIN, have been used for callus-mediated organogenesis of sweet potato (Table 2). Mukherjee (2002) reported that callus was induced on MS medium supplemented with 2.0 mg/l 2,4-D, and shoot organogenesis occurred from callus on MS medium supplemented with 200 mg/l NaCl. However, Kim et al. (2015) reported the callus-mediated organogenesis of sweet potato using internodes and young leaf explants and found that internodes were the better explant for callus-mediated organogenesis. Maximum callus induction occurred from internode explants grown on MS medium supplemented with 5.0 mg/l BA in combination with 1.0 mg/l NAA. Upon transfer to a fresh medium for shoot multiplication, it was observed that shoots and roots regenerated from the calli on the same medium (Table 2).

Rooting of *in vitro* regenerated shoots

For rooting, *in vitro* regenerated shoots of sweet potato were excised from the shooting medium and usually inoculated on MS medium or ½ MS medium without plant growth regulators (Matimati et al. 2005; Dugassa and Fevissa 2011; Doussoh et al. 2018a; Beyene et al. 2019; Dewir et al. 2020). However, a basal culture medium without any plant growth regulators was not sufficient for proper root development. Thus, MS or ½ MS medium supplemented with different concentrations of plant growth regulators has been used for the rooting of *in vitro* regenerated shoots by various researchers (Tables 1 & 2). Dugassa and Feyissa (2011) rooted *in vitro* regenerated shoots of sweet potato var. Awassa-83 on ½ MS medium supplemented with IBA (0.1 mg/l). Beyene et al. (2020) reported the use of the same half-strength MS medium but with a comparatively higher concentration of IBA (0.5 mg/l) for the rooting of red-peeled sweet potato. However, some authors also reported *in vitro*

regenerated shoots rooted in MS medium supplemented with different concentrations of NAA, IBA, and IAA either alone or in combination (Tables 1 & 2).

Somatic embryogenesis

Somatic embryogenesis plays a key role in micropropagation and provides a valuable tool for the genetic transformation of pharmaceutically and commercially important crop plants. Different types of explants, such as petioles, leaves, bud meristems, and lateral buds, have been used for somatic embryogenesis and subsequent plantlet regeneration of sweet potato (Table 3). Leaf explants have been frequently used for somatic embryogenesis by various researchers (Schultheis and Cantliffe 1992; Mukherjee 2002; Oggema et al. 2007; Sefasi et al. 2012; Masekesa et al. 2021). MS medium has been used as a preferred basal medium for callus induction, followed by the induction, maturation, and germination of somatic embryos. MS medium supplemented with different types and combinations of plant growth regulators, such as 2,4-D, KIN, and 2,4,5-T, has been used for the somatic embryogenesis of sweet potato. Studies have revealed that 2,4-D is preferred for embryogenic callus induction. These embryogenic calli were transferred to growth regulator-free MS medium or MS medium supplemented with different types of growth regulators, i.e., 2,4-D, abscisic acid (ABA) and KIN, and exhibited somatic embryo induction as well as maturation (Table 3). The somatic embryogenesis protocol is successful when the somatic embryo germinates and forms complete plantlets. Upon transfer to MS medium, ½ MS medium or MS medium supplemented with gibberellic acid (GA₃), or ½ MS augmented with BA, the somatic embryos formed plantlets (Table 3).

Synthetic seed technology

Ex situ conservation of vegetatively propagated plant species, including sweet potato, is a very difficult task (Doussoh et al. 2018b). Hence, the synthetic seed technique is the best alternative technique for the long-term conservation of commercially important and indigenous varieties of sweet potatoes (Tadda et al. 2022). Synthetic seeds obtained through alginate encapsulation of somatic embryos, node segments, shoot tips, and meristematic tissues could grow and form a whole plant under *in vitro* or *in vivo* environmental conditions (Behera et al. 2020). The ability of alginate-encapsulated explants to regrow is its most appealing characteristic. To date, the development of a synthetic seed protocol in sweet potato has rarely been reported. Chee and Cantliffe (1989) first developed a synthetic seed protocol for sweet potato using somatic embryos encapsulated in an alginate medium. Later, Mukherjee (2002) also reported a synthetic seed protocol for sweet potato using isolated single

Table 2 Callus mediated in vitro plant regeneration of sweet potato

Clone/cultivar/variety	Explant	Results	MS basal medium with plant growth regulators			References
			Callus induction	Shooting	Rooting	
<i>Ipomoea batatas</i> L	Leaf lamina	Callus induction, shoot regeneration	MS medium + 2,4-D (2.0 mg/l)	MS medium + NaCl (200 mg/l)	NI	Mukherjee 2002
<i>Ipomoea batatas</i> L	internode	Callus induction, shoot regeneration and rooting, plant formation	MS medium + BA (5.0 mg/l) + NAA (1.0 mg/l)	MS medium + BA (5.0 mg/l) + NAA (1.0 mg/l)		Kim et al. 2015
<i>Ipomoea batatas</i> L	Petiole	Callus induction	MS medium + 2,4-D (10 µM)	NI	NI	Rahman and Sultana 2017
<i>Ipomoea batatas</i> L. var. Kullufo	Lateral bud	Callus induction	MS medium + KIN (2.0 mg/l) + NAA (2.0 mg/l)	NI	NI	Mengs et al. 2018
<i>Ipomoea batatas</i> L. var. Tulla	Lateral bud	Callus induction	MS medium + KIN (2.0 mg/l) + NAA (2.0 mg/l)	NI	NI	Mengs et al. 2018

2,4-D- 2,4-dichlorophenoxyacetic acid, BA- N⁶-benzyladenine, KIN- kinetin, MS- Murashige and Skoog (1962) medium, NAA- naphthaleneacetic acid, NaCl- sodium chloride, NI- no information

somatic embryos. For encapsulation of somatic embryos, sodium alginate (2.5%) and calcium nitrate (2%) in ½ MS medium that was devoid of sucrose and organic nutrients was used. Successfully, 90–100% of the synthetic seeds were converted into plantlets and established in the field. Doussouh et al. (2018b) established a synthetic seed protocol based on the encapsulation-dehydration technique for short-term storage, conservation, and long-distance transport of two sweet potato landraces (i.e., Koïdokpon and Dokouicarotte). Synthetic seeds were made from shoot apices combined with sodium alginate (3%) and calcium chloride (1.32 M). The shoot apices were encapsulated before dehydration on silica gel for 5 and 6 h. The synthetic seeds were finally stored in batches in Eppendorf tubes at 2 °C for 15 days and 90 days. To check the survival and regeneration rate, the synthetic seeds were cultured on MS medium augmented with 0.15 mg/l BA + 0.2 mg/l NAA + 0.08 mg/l GA₃ + 80 mg/l adenine sulphate (ADS). The survival and regeneration rates of the synthetic seeds varied across landraces. The highest survival rate and regeneration rate observed were 59.26% & 37.04% and 37.04% & 11.11% in the landraces "Koïdokpon" and "Dokoui carotte", respectively. The synthetic seeds that were dehydrated for 6 h and stored for 15 days at 2 °C exhibited the best results in both cultivars. Recently, Tadda et al. (2022) reported a synthetic seed protocol using an in vitro nodal explant of sweet potato. The gel matrix and complexing agent were prepared using MS medium, and a combination of 4.0% sodium alginate (gel matrix) and 100 mM CaCl₂ (complexing agent) produced the best results. Alginate-encapsulated nodal explants or synthetic seeds cultured on different strengths of MS basal medium indicated that the highest percent (99%) of synthetic seed conversion into plantlets was found for ½ MS medium.

Acclimatization of in vitro regenerated plants

Acclimatization is the most important step in plant tissue culture. The tissue culture protocol is fruitful when in vitro regenerated plants are successfully acclimatized and transferred to the field with negligible mortality. During acclimatization, the survival rate of in vitro regenerated plants depends on the types and combinations of potting substrates. Different potting mixtures alone or in combinations have been used for the acclimatization and soil establishment of sweet potato with different success rates. Various combinations of potting substrates, such as a 2:1 ratio of river sand and sawdust, sawdust and rice mill waste, river sand and rice mill waste, river sand, rice mill waste, sawdust and jiffy peat, have been used for acclimatizing in vitro regenerated sweet potato plants. In vitro regenerated plantlets were acclimatized in pots containing rice husks and red soil (1:2), and approximately 80% of the plantlets were successfully established, as reported by Ogero et al. (2011). However, Ogero et al. (2012), while working with another two cultivars of sweet potato, Kemb-36 and Tainurey, used the same potting substrate (red soil and rice husk; 1:1) but reported differences in the survival rate between the two cultivars. A maximum of 67% of plantlets of the Tainurey cultivar survived, which was also low compared to their earlier report. A mixture of sterilized soil, vermiculite and sand (1:1:1) was used as a potting substrate by Gong et al. (2005), and plants survived successfully. Furthermore, Ubalua et al. (2013) reported that jiffy peat substrate was the most superior substrate for the acclimatization of in vitro plantlets with 100% success.

Table 3 In vitro plant regeneration through somatic embryogenesis of sweet potato

Clone/Cultivar/Variety	Explant	Results	MS basal medium with plant growth regulators				References
			Callus induction	Embryo induction	Maturation	Germination	
<i>Ipomoea batatas</i> L	Petiole	Callus induction, embryo induction, maturation, germination and plantlet formation	MS medium + 2,4-D (1.0 mg/l) + KIN (1.0 mg/l)	MS medium + 2,4-D (1.0 mg/l) + KIN (1.0 mg/l)	MS medium + KIN (0.25 mg/l)	MS medium	Tempton-Somers and Collins 1985
<i>Ipomoea batatas</i> L	Leaf	Callus induction, embryo formation, germination, and plantlet formation	MS medium + 2,4-D (0.5 mg/l)	MS medium + 2,4-D (0.5 mg/l)	MS medium + HCG (2.5%)	½ MS medium	Schultheis and Cantliffe 1992
<i>Ipomoea batatas</i> L, clone Q23728	Bud meristem	Callus induction, embryo induction, maturation, germination and plantlet formation	MS medium + 2,4-D (1.0 mg/l)	MS medium		MS medium	Sommino and Mini 1993
<i>Ipomoea batatas</i> L	Lateral bud	Callus induction, embryo formation and plantlet regeneration	MS medium + 2,4-D (10 µM)	MS medium + 2,4-D (10 µM)	MS medium + 2,4-D (0.01 µM) + KIN ((0.01 µM)	MS medium + KIN ((0.01 µM)	Cavalcante Alves et al. 1994
<i>Ipomoea batatas</i> L	Leaf	Callus induction, embryo production, maturation and plantlet formation	MS medium + 2,4-D (0.5 mg/l)	MS medium	MS medium + NaCl (5.0 g/l)	MS medium	Mukherjee 2002
<i>Ipomoea batatas</i> L, cv. Zapallo	Leaf	Callus induction, embryo induction, maturation, germination and plantlet formation	MS medium + 2,4-D (1.0 mg/l)	MS medium + ABA (2.0 mg/l)	MS medium + ABA (2.0 mg/l)	½ MS medium + BA (1.0 mg/l)	Oggema et al. 2007
<i>Ipomoea batatas</i> L, cv. Bwanjule	Leaf	Callus induction, embryo induction, and plantlet formation	MS medium + 2,4-D (0.05 mg/l)	MS medium + 2,4-D (0.05 mg/l)	MS medium + Zeatin riboside (0.2 mg/l)		Sefasi et al. 2012
<i>Ipomoea batatas</i> L, cv. Jewel, Jonathan	Lateral meristems	Callus induction, embryo formation, maturation, germination and plantlets formation	MS medium + 2,4,5-T (1.3 mg/l)	MS medium + ABA (1.0 mg/l)	MS medium + ABA (1.0 mg/l)	MS medium + GA ₃ (0.424 mg/l)	Manrique-Trujillo et al. 2013
<i>Ipomoea batatas</i> L, cv. Brondal	Leaf	Callus induction, embryo formation, maturation, germination and plantlets formation	MS medium + 2,4-D (0.5 mg/l) + KIN (0.1 mg/l) + Sucrose (30 g/l)	MS medium + 2,4-D (0.5 mg/l) + KIN (0.1 mg/l) + Sucrose (30 g/l)	MS medium + Sucrose (30 g/l)	MS medium + Sucrose (30 g/l)	Masekesa et al. 2021

2,4,5-T 2,4,5-trichlorophenoxyacetic acid, ½ MS half strength Murashige and Skoog (1962) medium, ABA Abscisic acid, BA N⁶ benzyladenine, GA₃ gibberellic acid, HCG hydroxyethyl cellulose gel KIN kinetin, MS Murashige and Skoog (1962) medium, NAA naphthaleneacetic acid, NaCl sodium chloride, NI no information

Biochemical analysis and genetic fidelity

In vitro plant propagation followed by its commercial utilization requires a high rate of genetic and biochemical uniformity among the micropropagated plants in comparison to that of the mother plant (Butiuc-Keul et al. 2016; Behera et al. 2018, 2019). The development of genetic and biochemical variation is a major drawback for in vitro plant regeneration through plant tissue culture (Alizadeh et al. 2015; Butiuc-Keul et al. 2016). Therefore, genetic fidelity and biochemical analysis of micropropagated sweet potato plants are essential for the development of successful micropropagation protocols aimed at their commercial utilization. To assess variations during tissue culture, several techniques have been used, such as morphological descriptions, cytological studies, isozyme studies (Gupta and Varshney 1999), and molecular markers, namely, Random Amplified Polymorphic DNA (RAPD) and Inter Simple Sequence Repeat (ISSR) markers. Genetic fidelity studies have rarely been reported for micropropagated sweet potato plants. Aboulila et al. (2008) reported a genetic fidelity analysis of tissue-cultured sweet potato plants compared to their mother plants using an RAPD marker and found 85.42% polymorphism between them. Later, Akomeah et al. (2019) studied the molecular variation of micropropagated sweet potato plants using a Methylation Sensitive Amplification Polymorphism (MSAP) marker and observed that all the tissue culture regenerated plants were genetically stable. Similar to genetic fidelity analysis, only two reports are available on the biochemical analysis of in vitro regenerated sweet potato plants in terms of dry matter, starch, sugar, and crude protein. Mukherjee et al. (2002) reported a comparative evaluation of yield and biochemical analyses, such as dry matter, starch, and sucrose. Their study revealed a low degree of variation among some of the in vitro regenerated plants and their respective mother plants. These variant regenerants were subsequently screened using isozyme markers, such as isozyme esterases, peroxidases, and acid phosphatases, and confirmed the stability of these variations. Delgado-Paredes et al. (2017) studied the biochemical analysis in terms of the stomatal chloroplast number, crude protein content, sugar, and dry matter of in vitro regenerated plants compared to mother plants, and they found that these in vitro regenerated plants were biochemically different compared to the mother plant.

Genetic improvement of sweet potato

It is necessary to understand the problems associated with sweet potato to enhance its yield and manage the food crisis at the global level. For the improvement of agronomically important traits or the development of nutrient-rich varieties, genetic engineering studies are essential. Liu (2017) reviewed details about the development of agronomically important traits in sweet potato using genetic engineering.

Tanaka et al. (2017) published a review paper on functional components in sweet potato and their genetic improvement. Kang et al. (2017) described the metabolic engineering of carotenoids in transgenic sweet potato in their review.

Conclusions and future prospects

Sweet potato is an important and well-known tuber crop in different regions of the world due to its nutritional and economic value. This plant species contains several varieties rich in different bioactive compounds, including anthocyanin and β -carotene. These plants are propagated vegetatively by stem or vine cutting and tubers; however, this method of propagation is time-consuming. Sometimes, the diseases associated with the mother plant are also transferred to the next generation during conventional methods of propagation, ultimately hindering the proper growth of the plant and its yield. Tissue culture has the potential to serve as an alternative method for the production of disease-free planting material on a large scale throughout the year. A number of in vitro plant regeneration protocols have been developed by different researchers across the globe for the production of disease-free planting material in various plant species. In this review, one of the focuses was on the study of different types of in vitro plant regeneration protocols involving meristem culture, callus culture, adventitious shoot organogenesis, somatic embryogenesis and synthetic seed technology. There is scope to further improve the different tissue culture-mediated plant regeneration protocols. Most importantly, the micropropagation protocols have not been well established for some of the important varieties of sweet potato, including 'Bhu Sona' (orange flesh), 'Bhu Krishna' (purple flesh), and 'Kisan' (white flesh). These varieties are in high demand by farmers as they are rich in β -carotene and anthocyanin. In addition, the techniques of shoot tip culture could be used by workers in the field to develop disease-free plants. Tissue culture-mediated biotechnological applications, such as synthetic seed systems for sweet potato, must also be developed to conserve landrace varieties for long-term conservation. As mentioned earlier, sweet potatoes are the source of a number of health-promoting phytochemicals. Thus, emphasis should be given to research including cell suspension culture, hairy root culture, bioreactor-based culture, and elicitation-based culture. Furthermore, extensive research is required on unexplored areas of sweet potato (Fig. 2), including the production of somaclonal variants with various agronomically important traits and homozygous lines for crop improvement programs.

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Data availability Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest regarding the publication of this manuscript.

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