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Therapeutic potentials and multi-omic advances towards utilization and improvement of genus *Physalis*

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Abstract

Physalis, a nutritionally rich therapeutic plant, is traditionally grown by subsistence farmers of Asia-Africa subcontinent. The genus contains so many species, among them many of them are cultivated and one wild species. All of these are valued for nutritional and therapeutic benefits. The ability of *Physalis* species to withstand severe environmental stresses is one of their key traits. They are also resilient to climate change since they can survive on very little food available for them. Worldwide, *Physalis* plants are grown in remote locations. This review centers on the diverse properties of *Physalis* species that are utilized by farmers and consumers for medical purposes. These properties have the potential to be improved upon, chosen for, and have pharmacological elements. Genome resources of *Physalis* have been thoroughly described in order to maximize biodiversity, investigate possible applications as phytomedicines, fulfil knowledge gaps, and capitalize on species variety to expedite global human nutritional security.

1. Introduction

Physalis are seen growing in warm temperate and subtropical climates worldwide. Globally, 100 known species are available of which six species have been reported from India (Deb, 1979), *viz.* (i) *Physalis alkekengi* L., (ii) *Physalis angulata* L., (iii) *Physalis ixocarpa* Brot. ex DC., (iv) *Physalis longifolia* Nutt., (v) *Physalis peruviana* L. as cultivated species, and (vi) *Physalis minima* L. as common weed. The production of a huge, papery husk from the calyx that partially or completely encloses the fruit is a notable characteristic of the plant (Martinez *et al.,* 2023; Jiang *et al.,* 2024). The fruit is small and orange in colour, resembling the form and structure of a small tomato. The *Physalis* genus is highly useful economically (Pretz and Deanna, 2020), not just because it produces food (as do allied solanaceous plants like Lycopersicon, Solanum, and Capsicum), but also because of its rich phytochemicals. Locally, *Physalis* is produced for its tasty and healthful fruit. *Physalis* species are rich suppliers of micronutrients, particularly minerals, according to chemical studies conducted by Musinguzi *et al.* (2007). Tropane alkaloids, such as tigloidine and tropine, and physalins, which are steroidal molecules, are the two main categories of phytochemicals. Plants belonging to the *Physalis* species have been utilized as therapeutic herbs for a long time. These plants have anti-inflammatory, diuretic, hepatoprotective, antiulcer, antimicrobial, antioxidant, and renal protective qualities. Tropane alkaloids are responsible for the antimuscarinic action. Limited information is available on the genetic diversity and therapeutic potential of the genus *Physalis* till date. The current review discusses the diversity of commonly found *Physalis* spp. and also discusses the production and biological activities of phytochemical constituents. In addition, advancements in omic techniques is briefly discussed to explain the diversity of the genus *Physalis.*

2. Genetic resources of *Physalis*

The cultivation and genomic resource composition of *Physalis* species are provided in Tables 1 and 2, respectively.

3. Properties and uses

The fruit of *Physalis* is quite adaptable; it can be eaten raw, roasted, or preserved in jams or jellies. Antioxidants, vitamin C, and other nutrients are abundant in it. These species contain minerals that are known to assist in regulating bodily functions, as well as many of the vitamins that are vital to human health.

3.1 *Physalis minima* L.

Physalis minima L., commonly called as bladder cherry, is a fast growing plant species found in India, Afghanistan, Tropical Africa and Australia (Kirtikar and Basu, 1991; Raju *et al.,* 2007). Its upright stem possesses ovate, delicate, toothed leaves and introverted pedicellate filiform flowers. The plant is 0.5-1.5 m in height, having

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dark green dorsal and light green ventral, ovate leaves of 9.7 cm long and 8.1 cm broad. The Indian Traditional System of Medicine claims it to be a significant medicinal herb. According to Sheriff *et al.* (2006), the abundance of phenolics and alkaloids in this species provides a strong source of antibacterial and antineoplastic potential. Various bioactive substances, including flavonoids, alkaloids, phenolics, and steroids, have been reported to be sourced from *P. minima* (Khare, 2007). Some important bioactive compounds like heneicosanoic acid, stearic acid, bicyclohepta-2, 4-dien octadecanoic acid (CAS), and octadeca-9, 12-dienoic acid have been identified in leaf extracts of *P. minima,* which justifies therapeutic potential of it (Karpagasundari and Kulothungan, 2014).

Table 1: Origin, distribution and cultivation of *Physalis* species

Species name	Region of origin/cultivation	Reference
P. minima	America, India, Pakistan, Bangladesh	Kirtikar and Basu, 1991
P. peruviana	Brazil, America, India	Kirtikar and Basu, 1991
P. alkekengi	India, Southern Europe, Japan	Deb, 1979
P. angulata	India, America	Deb, 1979
P. ixocarpa	India, Mexico, Central America	Deb, 1979
P. longifolia	India, North America	Deb, 1979
P. philadelphica	Mexico, Australia, South Africa	Del Monte and Díaz de, 1988

Table 2: *Physalis* genomic resources and features

Species	Ploidy	Chromosome number	Reference
P. minima	Tetraploid	2n = 4x = 48	Kumar *et al.,* 1989
P. peruviana	Tetraploid	2n = 4x = 48 (cultivated)	Nohra *et al.,* 2006
	Diploid	2n = 2x = 24 (wild)	Nohra *et al.,* 2006
P. alkekengi	Diploid	2n = 2x = 24	Yang and Zhou, 1998
P. angulata	Tetraploid	2n = 4x = 48	Ganapathi *et al.,* 1991
P. ixocarpa	Diploid	2n = 2x = 24	Cantwell *et al.,* 1992
P. longifolia	Tetraploid	2n = 4x = 48	Hinton, 1976
P. pruinosa	Diploid	2n = 2x =24	Badr *et al.,* 1997

P. minima bears yellow coloured, juicy berries as fruit with sweet and acidic tastes like a cherry tomato (Peter, 2007; Patel *et al.,* 2011). The nutritive berries are good starch sources (Patel *et al.,* 2011). In some places, the unripe berries are consumed after cooking as vegetables (Usher, 1974), while the ripe berries are taken to improve digestion because of their laxative characteristics (Chopra *et al.,* 1986). Berry contains about 6% carbohydrates and 2.7% protein with higher levels of vitamin C (Parmar and Kaushal, 1982). Studies demonstrated the anticancer activities of plant extracts (Duke and Ayensu, 1985).

3.2 *Physalis peruviana* L.

In both traditional and modern medicine, plant-derived medications are widely used and are becoming more so, particularly in developing nations. One of the plants most frequently utilized in traditional medicine globally is *Physalis peruviana* L. The plant *P. peruviana*, referred to as a golden berry, is a perennial herbaceous semi-shrub (Martinez, 1998). According to Ramirez *et al.* (2013), this species is primarily found in tropical areas of Peru and other hot, subtropical regions of the world. The species of *P. peruviana* is mostly cultivated in India and is reported to contain tetraploid (2n = 4x = 48) and hexaploid (2n = 6x = 72) chromosomes. Due to its dietary and medicinal values, extra attention is focused on this species. It has the potential to supply health-associated compounds present inside the fruits. Leaves and stems of *P. peruviana* are also considered rich sources of bioactive compounds to treat different ailments. Reports are available on use of *P. peruviana* as antidiabetic, antihepatitis, antiulcers, and for the treatment of various other ailments (Mayorga *et al.,* 2002; Arun and Asha, 2007). Reports on bioactive compounds with anti-inflammatory and antioxidant properties and the presence of vitamins are available in *P. peruviana* (Strik, 2007). This plant is known as an apoptosis inducer and has anticancerous properties. Yen *et al.* (2010) reported DNA damaging and chemotherapeutic effects of an important compound 4β-hydroxywithanolide (4βHWE), derived from stems and leaves of *P. peruviana*. This therapeutic compound also showed its efficiency against lung cancer. Therefore, this genus has attracted the interests of the researchers of the world recently. Despite the healing properties, the plant has a few extraordinary properties, including antipyretic, anti-inflammatory, antiallergic, antiulcer, antimicrobial, antioxidant, and antihepatitis (Ramadan *et al.,* 2011; Zhang *et al.,* 2013). Because of the high mineral, antioxidant, and diet content in berries of *P. peruviana,* this species is amongst the plant species with an excessive amount of nutritious value. Natural antioxidants from herbs, phytosterols, and essential fatty acids are abundant in the essential oil of *P. peruviana* (Ramadan and Moersel, 2003). Other than these, reports on *P. peruviana* have indicated the presence of other chemical substances, including phygrine, glycosides, withanolides, kaempferol, and quercetin (Ramadan and Morsel, 2007; Szefer and Nriagu, 2007; Borchani *et al.,* 2011).

3.3 *Physalis alkekengi* L.

Physalis alkekengi L. also called winter cherry with a height of about 25 inch, is an herbaceous perennial, erect and ascending herb with 3 inch long, ovate, and elliptic green leaves. *P. alkekengi* has been used usually for the management of coughs, sore throats, and ear infections in Korea, Europe, and China. Crude extracts and isolated compounds from *P. alkekengi* were found to possess a wide range of biological activities both *in vitro* and *in vivo*, including immunosuppressive, antibacterial, antileishmanial, antiinflammatory, antidiabetic, antioxidative, antimalarial, anti Alzheimer's disease, and vasodilatory properties (Laczkó-Zöld *et al.,* 2009: Hong *et al.,* 2015). Furthermore, the pertinent antitumor and antiinflammatory processes were clarified. *P. alkekengi* has a large degree of pharmacological potential, as indicated by the described actions. Reports on the anticancer effects of *P. alkekengi* are also available. It also possesses radical scavenging and lipid peroxidation inhibitory activity. According to the Unani System of Medicine, *P. alkekengi* fruit has analgesic, anthelmintic, anti-inflammatory, contraceptive, diuretic, hepatoprotective, and nephroprotective properties. Scar and wound healing are also improved by it. *P. alkekengi* fruits, along with a mixture of other plants, are used as a traditional medicine by tribal people living in the most remote area of the Indian subcontinent to treat kidney and bladder diseases of all kinds. It is one of the common practices of the Clod Desert Ladakh. Additionally, urine discharge, kidney haemorrhage, and inflammation are all well healed by it (Yang *et al.* 2022).

3.4 *Physalis angulata* L.

The Peruvian and Amazonian terms "mullaca" refer to *Physalis angulata* L., an annual shrub with branches commonly found in tropical and subtropical climatic conditions. It is a well-studied cytological plant with reported 2n=4x=48 chromosomes. *P. angulata* can attain a height of 1.0 m on average. The plant yields fruits that resemble golden pearls (Mejia and Rengifo, 2000). This important medicinal herb is being used for the treatment of various diseases, such as anaemia, rheumatism, stomach ache, kidney stones, prostrate, angina, diuresis, bladder inflammation, asthma, hepatitis by a large numbers of people (Mejia and Rengifo, 2000). According to Ruiz *et al.* (2011), cancer, bacteriemia, tumours, gonorrhoea, diabetes, infertility, and malaria may also be treated with the applications of *P. angulata*. This medicinal herb is also used to reduce fever and stop abortions during critical conditions. Because of the postpartum infectivity, Jovel *et al.* (1996) stated that the decoction of the leaves and fruits of *P. angulata* is used for "Tertian" in Peru. Additionally, *P. angulata* is recognized to possess antispasmodic and anti-inflammatory properties (Silva *et al.,* 2005). It has various useful substances, including flavonoids, alkaloids, steroids, and physalins (B, G, D, E, F, H, I, K, U, and V) detected in leaf, stem and fruits (Damu *et al.,* 2007; Chen *et al.,* 2011). Various withanolides (He *et al.,* 2007) as well as carotenoids (Rosso and Mercadante, 2007) were isolated from different plant parts, including stems, leaves and fruits of this important medicinal species, using methanolic extracts. There are also reports on its antimicrobial, antitumorous, anticancerous, antimalarial, anti-inflammatory, antileishmanial, hypotensive, and immunosuppressive properties (He *et al.,* 2005; Helvaci *et al.,* 2010; Sa *et al.,* 2011; Pinto *et al.,* 2010; Guimaraes *et al.,* 2010; Yu *et al.,* 2010). Additionally, the herb is said to have an antileishmaniasis function (Da Silva *et al.,* 2015). The total phenolic and flavonoid content, antioxidant activity, and *in vitro* anticancer potential of *P. angulata* leaf and fruit extracts were evaluated. The chemical makeup and structure of bioactive compounds found in extracts were examined using the GC-MS method. The anticancer activity data showed a concentration- and time-dependent decline in the percentage of viable anticancer cells. Additionally, the researchers observed changes in the morphology of the cells, which they attribute to the extracts of *P. angulata*. Using light microscopy, they saw that the number of HeLa cells started to decline as the concentration of ethanolic extract (fruit and leaves) increased (Pillai *et al.,* 2022).

3.5 *Physalis ixocarpa* Brot. ex Hornem

Since pre-Columbian times, *Physalis ixocarpa* Brot. ex Hornem has been grown as a crop in Mexico and Central America. Cytological analysis of *P. ixocarpa* revealed a diploid genotype with 2n=2x=24 chromosomes. *P. ixocarpa* extract is used to treat sore throats, cleanse the blood, strengthen the stomach, and protect against local poisoning (Khan and Jehan, 2015). In Mexico, the fruits of *P. ixocarpa* are referred to as "husk tomato" or "tomate verde" (green tomato). The fruits of *P. ixocarpa* are used to make flavorful sauces and stews. People from different parts of Mexico, the United States, and Central America enjoy the green fruits of this significant plant species. But in Mexico's west and centre, the purple fruits are eaten ((Mulato-Brito and Pena-Lomeli, 2007). The growing demand and exports of tomatillos, which are becoming more valuable in other nations, also contribute to their importance. Various methodologies are used to analyze the antimicrobial activities of plant extracts. During assessment of the antibacterial activity of plant extracts from different parts of *P. ixocarpa* prepared in aqueous and organic solvents, it has been observed that fruit and leaf extracts inhibited the development of *Klebsiella pneumoniae* and *Staphylococcus aureus*, whereas stem extracts effectively inhibited the growth of *Escherichia coli* and *Klebsiella pneumoniae*. Fruit extract in n-butanol and crude methanolic extract from the stem of *P. ixocarpa,* both shown inhibitory effects against *K. pneumoniae*. *P. ixocarpa* leaf crude methanolic extract exhibited antifungal activity (Khan *et al.,* 2016).

3.6 *Physalis longifolia* Nutt.

Physalis longifolia Nutt. often known as longleaf ground cherry or wild tomatillo is found mostly in United States, Southern Canada and Northern parts of Mexico. It is a tiny, herbaceous perennial plant that spreads *via* underground rhizomes. Because of its widespread distribution, it is regarded as a weed. It usually grows in grasslands, open woods, and ancient fields, but it also does well by roadsides and in disturbed areas. Researchers reported varying counts of chromosomes, *i.e.,* 2n = 4x = 48 (Tuteja and Bhatt, 1984) whereas 2n=2x=24 (Hinton, 1976) for *P. longifolia*. A study on biochemical constituents and biological activities of the dried fruit of *P. longifolia* was conducted, and HPLC analysis was used to identify the presence of withaferin A in the fruit. In an experimental mouse model, fruit extract led to a 60% volume reduction in breast carcinomas (MDA-MB-468LN). The reports highlight the potential anticancer action of *P. longifolia* fruits (Gallagher *et al.,* 2015).

3.7 *Physalis philadelphica* Lam.

According to Engels *et al.* (2006), *Physalis philadelphica* Lam. is native to Mesoamerica. A golden corolla and clavate stigma characterize this annual herb. Concerning usage and research, it is most likely the most advanced species now accessible. This species exhibits signs of domestication, as evidenced by the variation in its physical features (Olsen and Wendel, 2013). Commercially grown and wild types of husk tomatoes can easily be identified based on their phenotypic traits. Soil fertility affects the range of phenotypic traits. Zamora-Tavares *et al.* (2015) applied molecular markers across nine populations of *P. philadelphica* in Mexico and performed a genetic variability analysis. A higher level of the genetic diversity was observed among all populations studied, which is an indication of the existence of phenotypic variations in *P. philadelphica* due to variability among genetic makeup of them. A total of 216 constituents have been reported from the genus *Physalis* in the last few years (Zhang and Tong, 2016). These include physalins, withanolides, phytosterols, polyunsaturated fatty acids (PUFA), polyphenols, labdane, diterpenes, sucrose esters, flavonoids, ceramides, and others. As per information obtained from various publicly available databases, it was found that the active constituents of *Physalis* are not well studied, and only a few physicochemical properties of physalin A, B, D and F are reported as listed in Table 3. Oils derived from *Physalis* species include high levels of polyunsaturated fatty acids (PUFA). *Physalis* reports the presence of Fe and Zn as micronutrients, and vitamins A, B, and C along with macronutrients such as Mg, Ca, K, Na, and P. Alpha-, beta-, and β-carotene are the primary active forms of vitamin A found in fruits, along with â cryptoxanthin.

Table 3: Bioactive compounds present in different *Physalis* species

Species name	Compound	Reference
P. minima	n-Hexadecanoic acid, 2-[2-[2-[2-[2-[2-[2-(2-Hydroxyethoxy), O-Methyl-DL-serine, N-dimethylaminomethylene-, ethyl ester, Ethyl dl-(1-naphthyl) glycolate	Sasikala and Meena, 2016
	Heneicosanoic acid, Bicyclo Hepta-2, 4-dien Octadecanoic acid (CAS), Stearic acid, Octadeca-9, 12-dienoic acid	Karpagasundari and Kulothungan, 2014
	(Z)-3-Phenyl-2-propenoic acid, Octadecanoic acid, 2-Isopropoxyethyl propionate, 9,12,15-Octadecatrienoic acid, (Z, Z, Z)	Sasikala and Meena, 2016
P. peruviana	Linoleic, oleic, palmitic, γ-linolenic (GLA), and palmitoleic, ω-3 fatty acid (α-linolenic acid) and dihomo-γ-linolenic	Hassanien, 2011
	Phenolic compounds, flavonoids: rutin, myricetin, quercetin and kaempferol	Sathyadevi and Subramanian, 2015
P. alkekengi	Flavonoids	Liu *et al.*, 2015
P. angulata	Flavonol, Quercetin-3-O-glycoside, Kaempferol-3-O-glycoside, Phenolic acid	Medina Medrano *et al.*, 2015
P. ixocarpa	β-carotene and lutein	Elizalde-González and Hernández-Ogarcía, 2007
P. philadelphica	β-carotene and lutein	Elizalde-González and Hernández-Ogarcía, 2007

Physalis has been the focus of many research activities due to its historical use in the Ayurvedic medicine. In this regard, antitumor (Chen *et al.*, 2011; Reyes-Reyes *et al.*, 2013; Wu *et al.*, 2012), anti-inflammatory (Kang *et al.*, 2011; Pinto *et al.*, 2010), antimicrobial (Pietro *et al.*, 2000; Janurio *et al.*, 2002), antioxidant (Wu *et al.*, 2005), antimalarial (Sa *et al.*, 2011), antileishmanial (Choudhary *et al.*, 2007) and other therapeutic properties of *Physalis* have been demonstrated.

The phytochemicals obtained from the *Physalis* genus demonstrate positive biological qualities and could be exploited as lead molecules for the pharmaceutical sector to develop novel herbal formulations. The antioxidant and hypocholesterolemic activities of *Physalis* are conferred by the presence of phytosterols. However, physalins and withanolides provide anticancerous, anti-inflammatory, antibacterial, hepatoprotective, inmunomodulatory, and antiparasitic properties. In autoimmune illnesses, physalins can be used to suppress an undesirable immune response (Jyothibasu *et al.*, 2012). Bioassay (ChEMBL_972404) reports of physalin A, B, and F, showed their inhibitory bioactivity for NFKBIA (Inhibition of TNF alpha-induced l kappa B-alpha phosphorylation) in humans. Bioassay of physalin F on NR3C1 encoding for glucocorticoid receptor shows no activity (Brustolim *et al.*, 2010), while good activity against NFKBIA with activity value of 27.1 µM (Ozawa *et al.*, 2013; Jacobo-Herrera *et al.*, 2006).

Biochemical compositions related to the antioxidant properties of different *Physalis* species including *P. ixocarpa*, *P. peruviana*, *P. angulata* and *P. alkekengi* (González-Mendoza *et al.*, 2011; Rockenbach *et al.*, 2008; Wu *et al.*, 2009; Ismail and Alam, 2001; Cobaleda-Velasco *et al.*, 2017; Medina-Medrano *et al.*, 2015; Diaz *et al.*, 2012) have been demonstrated, respectively. Crude *Physalis* extracts have demonstrated many therapeutic actions and have significant potential for further medication development. Therefore, the phytochemical studies of other species should be done in order to harness the whole medicinal potential of this genus. Also, the genomic and transcriptomic data on *Physalis* will be useful for researchers for improvement of crop and bioactive metabolites in these plants.

Plant resources are currently used to make the nutraceutical and the functional foods that fight lifestyle disorders. Plant-derived bioactive components show promise as medicines with no negative side effects (Ho and Tan, 2011; Zhang *et al.*, 2005). A few *Physalis* species mediate erectile function, which is necessary for satisfying sexual desires. Men's erectile function controls their penile erection. However, erectile dysfunction (ED) has been observed to be common in both young and old men. Numerous factors, including blood pressure, iron deficiency, diabetes, hormonal imbalances, and physiological stress, have been linked to ED. Recently, Akomolafe *et* *al.* (2018) studied the enzymes associated with erectile dysfunction employing phenolics present in the species of *P. angulata* and *Newbouldia laevis*. They found that some of the genes related to the enzymes such as acetylcholinesterase (AchE), arginase, angiotensin-I converting enzyme (ACE-I) and Phosphodiesterase-5' (PDE-5') are up-regulated in ED sufferers (Huang *et al.*, 2013). These enzymes corroborate one of the means in the management of such erectile dysfunction. Synthetic inhibitors of aforesaid enzymes exert several harmful effects, though they are effective (Selvin *et al.*, 2007). Published reports suggest that phenolic constituents of the aqueous extract of *P. angulata* possess beneficial effects *in vitro*. ACE, a dipeptidyl carboxpeptidase (EC 3.4.15.1), related to peripheral hypertension, inactivates bradykinin (Wu *et al.*, 2006) and the condition changes into hypotension. The synthetic ACE inhibitors may cause cough, taste disturbances, rashes, and angioedema (Erdmann *et al.*, 2008). Therefore, plant derived ACE inhibitors are necessary for *in vivo* as well as *in vitro* systems (Gupta *et al.*, 2018; Wang *et al.*, 2016). Use of herbal extracts/functional food constitute an important parameter as a substitute of synthetic drugs. Particularly phenolic composition of *P. angulata* demonstrated appreciable levels of ACE-I inhibition *in vitro*.

The most ubiquitous cause of death of humans all over the world is the cancer of hepatocellular carcinoma (HCC). This cancer may arise due to the progressive accumulation of unusual mutations or gene products in the liver cells. Seeds of some of the pulses provide health promoting benefits in some of the prime diseases like diabetes, heart disease, and cancers (Roy *et al.*, 2010; Gautam *et al.*, 2018). Hassan *et al.* (2017) examined the role of the juice of *P. peruviana* on hepatocelluar carcinoma and found that HCC rats that received juice demonstrated improvements in physiological parameters. In addition, Cape gooseberry produced a significant role in hepatic disorders coupled with apoptosis. Further, aeroponically grown *P. peruviana* contained new withanoloids, experimentally found cytotoxic to the cells of the prostate and renal.

The concentration of bioactive compounds is influenced by environmental factors coordinated with harvest time and maturity state in many crop species. The aforesaid principal is also found in *Physalis* species. Bravo *et al.* (2018) performed a study to find out relations between bioactive compounds with cultivar type, and ripening time in *P. peruviana*. Their studies revealed that phenolic content was found to be affected by the time of harvest and state of maturity. Further, they advocated that fruits of *P. peruviana* be harvested on scheduled time employing prescribed environmental conditions (green house) to produce the highest portion of bioactive compounds. Now NMR-based profiling is targeted for generating metabolomics fingerprints. To trace the place of origin, NMR-technology can also be useful for identification of bioactive compounds present in the plants. Studies of Maruenda *et al.* (2018) engaged NMR to discriminate phytochemical differences among *P. peruviana* genotypes with their region of production. The *Physalis* plant has high potential biological application but only few scientific studies have been conducted. Some reports are available on findings of new bioactive compounds and patents have been granted to the researchers for the methods applied for their identification (Table 4).

Table 4: Patents on *Physalis* species

Species	Patent No.	Target	Inventor
Physalis longifolia	US20120196815 A1	Isolation of withanolides with anticancer activity	Timmermann *et al.*, 2012a
Physalis longifolia	WO2012106393 A3	Isolation of new withanolide	Timmermann *et al.*, 2012b
Physalis alkekengi	US20120102603 P1	Development of new variety 'Queen'	Uebelhart, 2012
Physalis alkekengi	USPP26585 P2	Development of new cultivar 'Prince'	Uebelhart, 2016
Physalis angulata	US20050101519A1	Process for isolating physalins	Tomassini *et al.*, 2005
Physalis minima	US8287921 B1	Development of formulations against cutaneous leishmaniasis	Rahman *et al.*, 2012
Physalis minima	EP2689767 A1	Development of cosmetic composition	Dryer and Ptchelintsev, 2004

Chemical databases like ChEMBL and Pubchem, have limited information about active constituents of this plant, as presented in the above text. These databases also lack information about the targets of active constituents of *Physalis*. Biological assay information is also not represented by these databases.

4. Multi-omic advancements in *Physalis*

4.1 Genomics

Physalis species are habitually grown in a few or selected parts of the world. These species can serve as valuable resources to find out important genes because some of them are weeds. Due to the weedy nature of many *Physalis* strains, they are valued for wide agronomic traits such as drought tolerance, salinity tolerance, water logging tolerance, and resistance to various biotic stresses. The technological developments in the field of molecular biology using DNA barcoding, molecular markers may be used to classify the *Physalis* landraces. To shorten the time period, it is essential to combine conventional information with advanced genomics techniques to describe assortment for crop improvement (Velraj *et al*., 2024). The distinctive feature of the genus *Physalis* is its innovative post-floral morphology. Furthermore, there is a remarkable unevenness in the fruit's size, colour, and flavour. To understand the developmental genetics of *Physalis* fruits, a variety of research projects have been carried out, including gene identification and isolation, expression, protein interactions, genetic transformation, and virus-induced gene silencing by many researchers (Zhao *et al.*, 2013; Wang *et al.*, 2014). As a result of these studies, *Physalis* is a matter of research as a model plant system for the study of plant evolution and ecology (Zhang *et al.*, 2014a,b; Li and He, 2015).

There are few reports on the use of molecular markers for molecular variability analysis of *Physalis* species. The usage of random amplified microsatellites (RAMs) is present in the literature. High genetic diversity and heterozygosity were found in the study, which involved a collection of 43 biotypes from five distinct geographic sites in Colombia (Mun˜oz Flo´rez *et al.,* 2008). Further, RAM markers have been used for genetic diversity analysis among *P. peruviana* genotypes (Betancourt *et al.,* 2008; Morillo Paz *et al.,* 2011). In a separate study, a total of 1133 (932 imperfect, 201 perfect) microsatellites belonging to untranslated regions and a total of 387 (304 imperfect, 83 perfect) microsatellites belonging to coding regions from the leaf transcriptome of *P. peruviana* were identified. Some microsatellites belonging to untranslated regions were applied for further amplification with seven ecotypes of *P. peruviana* belonging to Colombia, Kenya, and Ecuador with one closely associated species, *P. floridana.* The microsatellite set developed in the study may be useful in the future improvement of *P. peruviana* species (Simbaqueba *et al.,* 2011). In advance molecular marker technology, single nucleotide polymorphism (SNP) is important to study the population structure of *Physalis*. In this regard, 642 SNP markers were identified (Table 5) and used for the genetic diversity analysis of 47 accessions of *P. peruviana* from Columbia (Garzón-Martínez *et al.,* 2015).

Table 5: Genetic diversity studies using different molecular markers in *Physalis*

Species	Markers	Objective	Reference
P. minima	ISSR	Genetic diversity and variation analysis	Usaizan *et al.,* 2014
	RAPD	Genetic diversity and variation analysis	Pagare *et al.,* 2017
P. peruviana	SSR, COS, PIP, InDel	Species transferability	Wei *et al.,* 2012
	SSR	Development of SSR	Simbaqueba *et al.,* 2011
	EST-SSR	Identification of SSR	Garzón-Martínez *et al.,* 2012
	InDels, SNPs	Genetic diversity analysis	Garzón-Martínez *et al.,* 2015
	RAM	Genetic diversity analysis	Bonilla *et al.,* 2008
	RAM	Genetic diversity analysis	Morillo Paz *et al.,* 2011
	ISSR	Genetic variability analysisSpecies delimitation	Medina-Medrano *et al.,* 2016
	SSR	Genetic structure analysis	Chacón *et al.,* 2016
	ITS1, ITS2	Phylogenetic relationship	Jalab and Al Rufaye, 2024
P. philadelphica	ISSR	Genetic diversity analysis	Zamora-Tavares *et al.,* 2015
P. ixocarpa	Morphological	Fruit quality evaluation	Ramírez-Godina *et al.,* 2013
P. nicandroides	SSR, COS, PIP, InDel	Genetic diversity, Species transferability	Wei *et al.,* 2012
P. angulata	SSR, COS, PIP, InDel	Genetic diversity, Species transferability	Wei *et al.,* 2012
	ISSR	Genetic variabilitySpecies delimitation	Medina-Medrano *et al.,* 2016
	ITS1, ITS2	Phylogenetic relationship	Jalab and Al Rufaye, 2024
P. acutifolia	SSR, COS, PIP, InDel	Genetic diversity, Species transferability	Wei *et al.,* 2012
P. pubescens	SSR, COS, PIP, InDel	Genetic diversity, Species transferability	Wei *et al.,* 2012
P. solanacea	ISSR	Genetic diversity, Species delimitation	Medina-Medrano *et al.,* 2016
P. patula	ISSR	Genetic diversity, Species delimitation	Medina-Medrano *et al.,* 2016
P. subulata	ISSR	Genetic diversity, Species delimitation	Medina-Medrano *et al.,* 2016

ISSR-Inter simple sequence repeat, COS-conserved ortholog sets, SSR-Simple sequence repeat, PIP-potential intron polymorphism, InDel- insertion/deletion, SNP-Single nucleotide polymorphism, RAM-Random Amplified Microsatellites

Species transferability of molecular markers is important to know the presence of similar sequences in different species. Beneficial genes may be transferred from one species to another because of similarity in sequences. Wei *et al.* (2012) used SSR, COS, PIP and InDel for species transferability studies among *P. peruviana, P. nicandroides, P. angulata, P. acutifolia*, and *P. pubescens*. Very few reports are available for *P. minima,* but more are beginning to appear in the literature. In Malaysia, 130 genotypes of *P. minima* were collected from different geographical regions and characterized using ISSR markers. A higher level of molecular diversity was found among the studied genotypes (Usaizan *et al.,* 2014). A total of 88 ISSR markers were used to identify diversity among nine populations of wild, weedy, and cultivated *P. philadelphica*. A higher level of genetic diversity at the DNA level was detected among populations with 91% polymorphic loci. Among all, 68% polymorphic loci were found in the wild gene pool however, 81% in weedy and 77% in the cultivated pool (Zamora-Tavares *et al.,* 2015). Out of 60,663 SNPs identified in *P. peruviana*, using genotyping by sequencing (GBS). Osorio-Guarin *et al.* (2016) reported the presence of 16 and 12 disease resistant markers in *P. peruviana* by taking tomato and potato genomes, respectively, as references. These markers can be used for breeding and improving *Physalis*. The structural diversity of 85 accessions of cape gooseberry (*Physalis*) was analysed by Chacon *et al.* (2016) in Colombia using 15 SSR makers and found that the highest polymorphism information content (PIC=0.568) was given by SSR15 marker. Recently, Jalab and Al Rufaye (2024) identified a phylogenetic relationship among *P. peruviana* and *P. alkengi* using ITS1 and ITS2 markers. Both of these markers are used for species identification and DNA barcoding of plants.

4.2 Transcriptomics

Next-generation sequencing (NGS) technology provides a platform technology, for sequencing DNA and RNA for model/non-model organisms without prior genomic data (Su *et al.,* 2011). Gene discovery, genome annotation, and determination of phylogenetic relationships can be done with the use of expressed sequence tags (ESTs) markers (Blanca *et al.,* 2011). With the use of 454 GS-FLX Titanium technology, the transcriptome of a *P. peruviana* leaf was studied for the first time. A mean of 371 nucleotides was produced by 652,614 ESTs derived from the *P. peruviana* leaf cDNA collection. The reference plants for EST predictions in *P. peruviana* were *Solanum lycopersicum* (tomato) and *Solanum tuberosum* (potato). Furthermore, according to Garzón-Martínez *et al.* (2012), the species diversity from assembled ESTs was identified. An analysis of transcriptome-wide variation in *P. philadelphica* floral organ size was conducted (Wang *et al.,* 2012) and the primary cause of variation was determined to be changes in the expression capacity of a few important regulatory genes during the developmental process. Transcriptome analysis of *P. peruviana* and *P. alkekengi* leaves revealed the presence of 54513 and 75221 unigenes, respectively. Furthermore, thousands of SSRs were identified in *P. alkekengi* and *P. peruviana* (Fukushima *et al.,* 2016).

4.3 Metabolomics

Metabolomics is one of the key disciplines within the field of "omics" sciences. The profile of metabolites in a sample at a given point in time, stage, or environmental condition can be determined using metabolomics, which is helpful in understanding the physiological state of an organism and its functional role. Therefore, it is believed that metabolomics can close the gap between genetics and phenotype. There are not many reports on metabolomics in *Physalis*. *P. pubescens* is a fruit plant known for its herbal benefits to human health. A number of techniques were employed, including time-of-flight mass spectrometry coupled to quadrupole with ultra performance liquid chromatography (UPLC-Q/TOF-MS), to determine which metabolites were responsible for the antioxidant and antifatigue effects of *P. pubscens* in rats after oral administration. The study found that a total of fifteen metabolites may be biomarkers. Additional UPLC-Q/TOF-MS studies showed that antioxidant and antifatigue properties of *P. pubscens* are caused by modifications in energy and amino acid metabolism (Chu *et al.,* 2015).

4.4 Tissue culture and genetic transformation

The technique of tissue culture holds significant value in the micropropagation and preservation of medicinally valuable plants. The future standardization of tissue culture and genetic transformation techniques is required due to the diverse therapeutic activities of *Physalis*. Various reports are available on *in vitro* culturing of *Physalis* species (Table 6).

Table 6: Tissue culture reports available in *Physalis*

Species	Explant	Medium	Reference
Physalis minima	Shoot tip	MS + 0.3 mgl^{-1} NAA	Afroz *et al.,* 2009
	Leaf	MS + 2, 4-D (0.4 mgl^{-1})	Mungole *et al.,* 2011
	Nodal	MS + 0.5 µM BA	Intzaar *et al.,* 2013
	Nodal	BAP (2.0 mgl^{-1}) + NAA (1.5 mgl^{-1}) + GA3 (0.5 mgl^{-1})	Ramar and Ayyadurai, 2014
	Leaf	BAP (2.5 mgl^{-1}) + IAA (1 mgl^{-1}) + KIN (1 mgl^{-1})	Ramar and Ayyadurai, 2014
	Nodal	MS + 2.0 mgl^{-1} BAP + 0.25 mgl^{-1} IAA	Sheeba *et al.,* 2015
	Leaf	MS + 9.0 µM 2,4-D + 4.5 µM Kn	Azlan and Marziah, 2015
	Nodal	MS + 1.0 mgl^{-1} IBA (95%)	Sandhya and Rao, 2015
Physalis peruviana	Nodal	LS + 0.5 mgl^{-1} TDZ	Yücesan *et al.,* 2015
	Nodal	MS + 2.0 mgl^{-1} BAP + 1.0 mgl^{-1} GA3 + 1.0 mgl^{-1} 2, 4-D	Ramar *et al.,* 2014
	Leaf	MS + 3.0 mgl^{-1} BAP+1.0 mgl^{-1} GA3+ 1.0 mgl^{-1} 2, 4-D	Ramar *et al.,* 2014
	Leaf	MS + 2 mgl^{-1} BAP + 2 mgl^{-1} Kin	Otroshy *et al.,* 2013
	Nodal	MS + 4 mgl^{-1} BAP + 1 mgl^{-1} Kin + 0.5 mgl^{-1} IBA	Otroshy *et al.,* 2013
	Leaf	MS + 2% sucrose + 4.0 mgl^{-1} NAA + 1.0 mgl^{-1} BA	Gautam *et al.,* 2011
Physalis ixocarpa	Hypocotyl	MS + 12.5-25 M BA + 5 M NAA	Ramirez-Malagónand Ochoa-Alejo, 1991
	Nodal	MS + 1.5 mgl^{-1} BAP	Khan and Bakht, 2015
Physalis angulata	Axillary meristem	MS + 1.5 mgl^{-1} (IAA) + 0.25 mgl^{-1} (GA_3)	Kumar *et al.,* 2015
Physalis pubescens	Shoot tip	MS + NAA 0.125 mgl^{-1}	Yousry, 2013

Ramirez-Malagon and Ochoa-Alejo (1991) used hypocotyl explants and MS + 12.5-25 M BA + 5 M NAA for regeneration purposes in *P. ixocarpa*. In *P. peruviana,* MS + 2% sucrose was used for callus production. In comparison to the explants, nutrient media supplemented with 4.0 mgl^{-1} NAA and 1.0 mgl^{-1} BA showed superior callus growth with significant secondary metabolite synthesis (Gautam *et al.,* 2011).

In a different study, different concentrations of BAP and Kin were employed for leaf explants while BAP and Kin were combined with IBA for nodal segments to examine the impact of growth regulators on plant regeneration on *P. peruviana* MS media. When using both kinds of explants for regeneration, higher quantities of BAP and Kin were shown to be more successful (Otroshy *et al.,* 2013). For the effective *in vitro* regeneration of *P. peruviana* from node, internode, and leaf explants, MS medium + B5 vitamins and various quantities of PGRs, such as BAP, GA3, and 2,4-D, were utilized. The nodal and internodal explants cultured on 2.0 mgl^{-1} BAP + 1.0 mgl^{-1} GA3 + 1.0 mgl^{-1} 2, 4-D produced the greatest number of multiple shoots. Leaf explants on 3.0 mgl^{-1} BAP + 1.0 mgl^{-1} GA_3 + 1.0 mgl^{-1} 2, 4-D showed a significant frequency of shoot multiplication (Ramar *et al.,* 2014). Using nodal segments, an effective regeneration strategy for *P. peruviana* was created. Direct plant regeneration was discovered in this experiment on LS medium with either 0.25 mgl^{-1} IAA in combination with 0.5 mgl^{-1} BAP, Kin, TDZ, or GA_3 alone (Yücesan *et al.,* 2015). For the nodal and intermodal explants, 2.5 mg ml^{-1} BAP and 0.005 mg ml^{-1} IBA were reported to work well in a related trial (Singh *et al.,* 2016).

Tissue culture practices for micropropagation and multiplication purposes were also applied to *P. minima.* Researchers used shoot tips (Afroz *et al.,* 2009; Yousry, 2013), leaf (Sheeba *et al.,* 2010; Mungole *et al.,* 2011; Ramar and Ayyadurai, 2014; Azlan and Mahmood, 2015) and nodal segments (Ramar and Ayyadurai, 2014; Sheeba *et al.,* 2010) as explants for protocol standardization and multiplication of *P. minima*. 2, 4-D and kinetin were used to create callus cultures from *P. minima* leaf, stem, and root explants (Azlan and Marziah, 2015). Optimizing the composition of the media and the cell explants, including the basal media, salt concentrations, carbon sources, and plant growth regulators, led to an increase in callus growth and the production of the anticancer compound physalin B. According to Azlan and Marziah (2015), the optimal way to initiate callus cultures obtained from leaf, stem, and root explants was to use 9.0 µM 2, 4-D, and 4.5 µM kinetin.

Using axillary meristem explants, the best plant propagation procedure for *P. angulata* has been determined. In this sequence, on MS media with 0.5-2.5 mgl^{-1} BAP/Zeatin/KIN, shoot bud proliferation was observed (Owk *et al.,* 2015; Owk *et al.,* 2016). On 1.0 mgl^{-1} GA_3 and 1.0 mgl^{-1} IBA, respectively, successful shoot elongation and roots were observed.

Transgenic protocols for *P. minima* utilizing *Agrobacterium rhizogenes* (Azlan *et al.,* 2002) and *Agrobacterium tumefaciens* (Sheeba *et al.,* 2010). Such techniques have allowed *P. minima* plants to produce higher amounts of pharmaceutically important compounds and to be improved for abiotic stress tolerance and disease resistance. Transformed plants of *P. ixocarpa* were obtained by regeneration from hairy roots transformed with *A. rhizogenes* ATCC 15834 (Bergier *et al.,* 2012). Studies on genetic transformation are presented in Table 7.

Table 7: Genetic transformation in *Physalis*

Species	Bacterium	Strain	Reference
P. minima	*Agrobacterium rhizogenes*	LBA9402	Azlan *et al.,* 2002
	Agrobacterium rhizogenes	LBA9402	Azlan *et al.,* 2002
	Agrobacterium tumefaciens	LBA 4404 pB19	Sheeba *et al.,* 2010
P. ixocarpa	*Agrobacterium tumefaciens*	C58C1 pTiC58	Garcia *et al.,* 1992
	Agrobacterium rhizogenes	ATCC 15834	Bergier *et al.,* 2012
P. floridana	*Agrobacterium tumefaciens*	GV3101	Zhang *et al.,* 2014

5. Conclusion

The fruit of *Physalis*, a source of metabolites exhibiting various biochemical activities, is a useful medicine and food supplement that has provided the global population with an economic way to use whole fruit for human consumption. Even though *Physalis* has a large genetic diversity, its benefits are not well understood in many parts of the world. *Physalis* is a weed in many species. Investigating its wild forms as a potential source of medicinal compounds is crucial. Biotechnology holds great potential for enhancing the genetic diversity and bioactive metabolites of *Physalis*, as well as for boosting the genetic resources of the organism. However, advancements in high-throughput proteomics and metabolomics methods, in addition to the fusion of several omics approaches, are expected to revolutionize the complex biological systems observed in *Physalis*. It will improve basic understandings of the molecular basis of stress tolerance in these crops in addition to aiding in the large-scale discovery of genes, proteins, and metabolites involved in various molecular and signalling networks. Thus, to prepare for future studies, it is imperative to conduct these kinds of investigations in *Physalis* in great detail. A coordinated effort involving all omics will be crucial to understanding the stress tolerance mechanism in *Physalis*, which can then be used for traditional breeding or marker assisted selection. There has been no report on gene pyramiding thus far on *Physalis* quantitative trait loci (QTL) mapping, which is currently in its early stages. Greater genome sequence and EST availability will be crucial for QTL mapping and other breeding techniques. Therefore, the current state of affairs can be improved, and it will be feasible to target *Physalis* for the genetic enhancement. Advancements in omics technologies, transgenic technology, and MAS are playing a major role in the improvement of *Physalis*. Utilizing modern genetic techniques could aid in the exploitation of biodiversity.

Though, the phytochemical constituents of *Physalis* have immense therapeutic potential, scanty information is available on active constituents and their target sites. Further research is needed on biological assays using phytochemical constituents of *Physalis* so that genetic network analysis and biological activity profiling can be performed to study various genetic interactions using the bioinformatics approach. The upcoming advanced technologies like next generation sequencing, the bioinformatics, and further use of genetic engineering can help to provide a way to improve the wild varieties of *Physalis* and make them fit for human consumption.

Conflict of interest

The authors declare no conflicts of interest relevant to this article.

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