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Production, Genetics, Postharvest Management and Pharmacological Characteristics of *Sechium edule* (Jacq.) Sw.

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ABSTRACT

The Cucurbitaceae family represents an important group of domesticated plants including the genera *Cucumis*, *Momordica*, *Luffa*, *Lageraria*, *Citrullus*, and in Central America *Cucurbita* and *Sechium* stand out because of their nutritious and economic value. *Sechium edule* (Jacq.) Sw., commonly called chayote, is highlighted in this review. The importance of chayote is based on the growing commercial demand of the fruit and its large-scale production in Mexico and Costa Rica, and to a lesser extent, in Guatemala, Brazil, Puerto Rico, Algeria, India, New Zealand, and Australia. Chayote comes from the cloud forest of Mexico and Central America, the central region being the State of Veracruz, Mexico, where the largest infraspecific variation has been identified, recently classified in botanical varieties with different shape, color, and flavor. Despite the large variety, only the chayote called smooth green (*Virens levis*) has been utilized for large-scale commercial exploitation. For this variety, research has been carried out with respect to traditional and commercial production systems, ecophysiological behavior, disease identification and diagnosis (under field and storage conditions), postharvest technology, medicinal and nutraceutic use, and regulations for international trade, topics referred to in this review.

Keywords: chayote, infraspecific variation, medicinal use, storage, varieties
Abbreviations: AMPc, adenosine, 3,5-monophosphate cyclic; **CCl_4**, carbon tetrachloride; **ED_{50}**, effective dose 50; **GISeM**, Grupo Interdisciplinario de Investigación en *Sechium edule* en México; **GMPc**, guanosin-monophosphate cyclic; **GPT**, glutamate-pyruvate transminase; **KB, HeLa**, **P-388** and **L-929**, sensible cells to cytotoxicity; **MS**, Murashige and Skoog

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Invited Review

INTRODUCTION

Phytogenetic resources for food and agriculture constitute the biological base of world-wide food security. These resources are found in the diversity of genetic material present in wild relations, traditional and modern varieties (Padulosi *et al*. 1999). The interest in studying these resources lies in the fact that they are fundamental to feed the world population. The farmers and breeders utilized these commodities to improve the quality and the productivity of their crops (FAO 2004). The importance of phytogenetic resources in agriculture and food consists in the large quantity of benefits which are obtained from them. Padulosi (1998) considered that agro-biodiversity may have represented around the 7000 species with potential use for food, which did not surpass the 10% mark. Mexico is a country of great biological riches and located among the planet's countries of mega-diversity (Rzedowski 1993), with approximately 22,000 endemic species, being the center of origin and domestication of between 66 and 102 cultivated species, multiplied by their different varieties (Ortega-Paczka *et al*. 1998), with a large number of races, many of them semi-domesticated and wild relations (Hernández 1985).

One of these species is chayote (*Sechium edule* (Jacq.) Sw.), originating from Middle America, Mexico being the place of greatest biodiversity (Cruz-León 1985-1986; Ortega-Paczka *et al*. 1998). Chayote is practically spread-out over the five continents since in the last twenty years this species has commercially prospered from a backyard vegetable to an untraditional export product (Flores 1989; Cadena-Iñiguez *et al*. 2001), with an increase in its demand of consumption in Unites States and Canada. The preference for chayote on these markets as an import product has been set in fourth place after avocado, tomato, and coffee, in the case of Mexico (Bancomext 2004). The producer countries are Mexico, Costa Rica, Brazil and the Dominican Republic with 360, 170, 50 and 2.3 thousand tons. Costa Rica exports around 40% of its production, 33,000 t to the Unites States and Canada, and 35,000 t to different countries in Central America, the Caribbean and Europe (CNP 2007). Mexico exports 109,000 t to the US and Canada (SNIIM 2004).

ORIGIN AND DISTRIBUTION

Different from what happens with other cultivated species, in *S. edule* there is no archaeological evidence or there are not any relicts permitting to specify the age of its origin and management, due to the soft testa of its seed and its fleshy fruit, which cannot survive (Lira 1995). The main evidence of its origin is the existence of wild chayotes in the central region and the south of Mexico and Central America. It is assumed that the modern term chayote is a modification of the Náhuatl words "huitz ayotl", "chayotl", and "chayotli" (prickly pumpkin), which would confirm its use since pre-Columbian times (Cook 1901). The importance of genus *Sechium* (P.Br.) is supported by the species *S. edule* (Jacq.) Sw. and *Sechium tacaco* (Pitt.) C. Jeffrey, being of nutritious importance, since the fruits of both species and the root of the first formed part of the diet of pre-Columbian cultures (Hernández 1985; Lira-Saade 1996). The European naturalist, Francisco Hernández, who lived in Mexico during the period between the 15th and the 16th century (Cook 1901), was one of the first to inform about the existence of chayote. After the conquest of Mexico, many species of nutritional importance, such as bean, maize, peppers, tomato, pumpkin, and chayote, were transferred to different regions of the Spanish empire, starting their distribution outside their center of origin. According to the data mentioned by Browne (1756), which is based on the information of Sloane (1689) and quoted by Cook (1901), it is believed that chayote was introduced to the Islands of Cuba, Jamaica, and Puerto Rico by the Spanish. Because of its nutritional value and its easy adaptation to environmental conditions, it was transferred to regions like California, Louisiana, Hawaii and Philippines, and Florida at the end of the 19th century (Reinecke 1898).

TAXONOMY AND INFRASPECIFIC VARIATION

S. edule is an uprising perennial plant with tendrils and tuberous roots. Its stems are several meters long, slightly compressed and longitudinally furrowed; green, when they are young, and brownish-gray at maturing; each knot has a leaf, one unisexual inflorescence, and a tendril ramified in two and up to five smaller branches. The leaves with long petiole are simple, lobed or angular, palm-shaped with branched vein structure. Flowers are unisexual, axillary and occasionally staminate and pistillate at the same knot, or flowers of both sexes on the same axis. The fruit is pendulous, large, obovoid or pyriform, with a variable number of longitudinal depressions, white surface, light or dark brilliant green; it may be glabrous, with fine hair or with a variable number of spines and only one seed (Maffioli 1981; Flores 1989; Lira-Saade 1996). During many years it was assumed that *Sechium* was a monotypic genus, whose only species was *S. edule* Swartz; Jeffrey (1978) however, included six other species with the sections *Frantzia* and *Polakowskia*. Despite Jeffrey's efforts (1978) to merge some genera and species related to *Sechium*, several authors considered that at least *Polakowskia* and *Frantzia* are rather distant from the originnal center of *Sechium* and are taxonomically different. The following taxa are considered synonyms for *Sechium*: *Sicyos edulis* Jacq., *Chayota edulis* Jacq., *Sechium Americanum* Poir., *Cucumis acutangulus* Descourt., and *Sechium chayota* Hemsley (Flores 1989; Lira and Chiang 1992) though these have fallen into disuse. Recently it has been accepted that within the genus *Sechium* there are ten species, eight of which are wild (*S. chinantlense*, *S. compositum*, *S. hintonii*, *S. talamancense*, *S. panamense*, *S. pittieri*, *S. venosum*, *S. vilosum*) and two cultivated (*S. tacaco* and *S. edule*), which are divided up from Mexico to Panama (Lira-Saade 1996).

An important feature in the species is its broad variation with respect to form and color of fruits, many of which are only known on local markets. The economic importance of each chayote type is mainly based on local preference, which – though in most cases it is very limited – has permitted to maintain its phenotypic identity and ethno-botanical nomenclature. Cook (1901) recognized on the Caribbean islands "varieties" of green and cream-yellow chayote growing in the high and cool parts; he also identified pyriform and spherical fruits as well as differences in size and coloring of flowers; the cream-white "varieties" had small white flowers, whereas the flowers of the green fruits were larger and yellow. Although the settlers had incorporated them into their diet, they did not cultivate them. Later, basing on Gardener's Chronicle and Agriculture Gazette (1865) Cook found in Puerto Rico what he called five "varieties", which he described by their morphological variation as "Round white", "Pointed green", "Broad green", and "Oval green". In Mexico, popular nomenclature classifies chayotes by their color, as "black" those of dark green epidermis, "green" those of light green, and "white" the ones of cream-yellow epidermis; by their appearance (smooth or prickly), and by their flavor ("neutral", "sweet", and "bitter") (Cadena-Iñiguez 2005).

In an effort to put the infraspecific complex presented in *S. edule* in order, Lira *et al*. (1999) proposed a new taxonomic arrangement, grouping the cultivated types in the subspecies *S. edule* ssp. *edule* and the wild one as *S. edule* ssp. *silvestrys*. These authors based this separation on the morphological and chromosomal differences through identification of karyotypes in pollen grains. Regrettably, in this proposal it was not indicated which cultivated type or types were included in the analysis, infraspecific hybrids, and products of spontaneous crossings among chayotes, with different phenotypes and degrees of domestication, possibly being involved, since there is no high genetic differentiation that limits crossing-over among the types, in *Sechium edule* this crossing is common because there is no synchroniza-

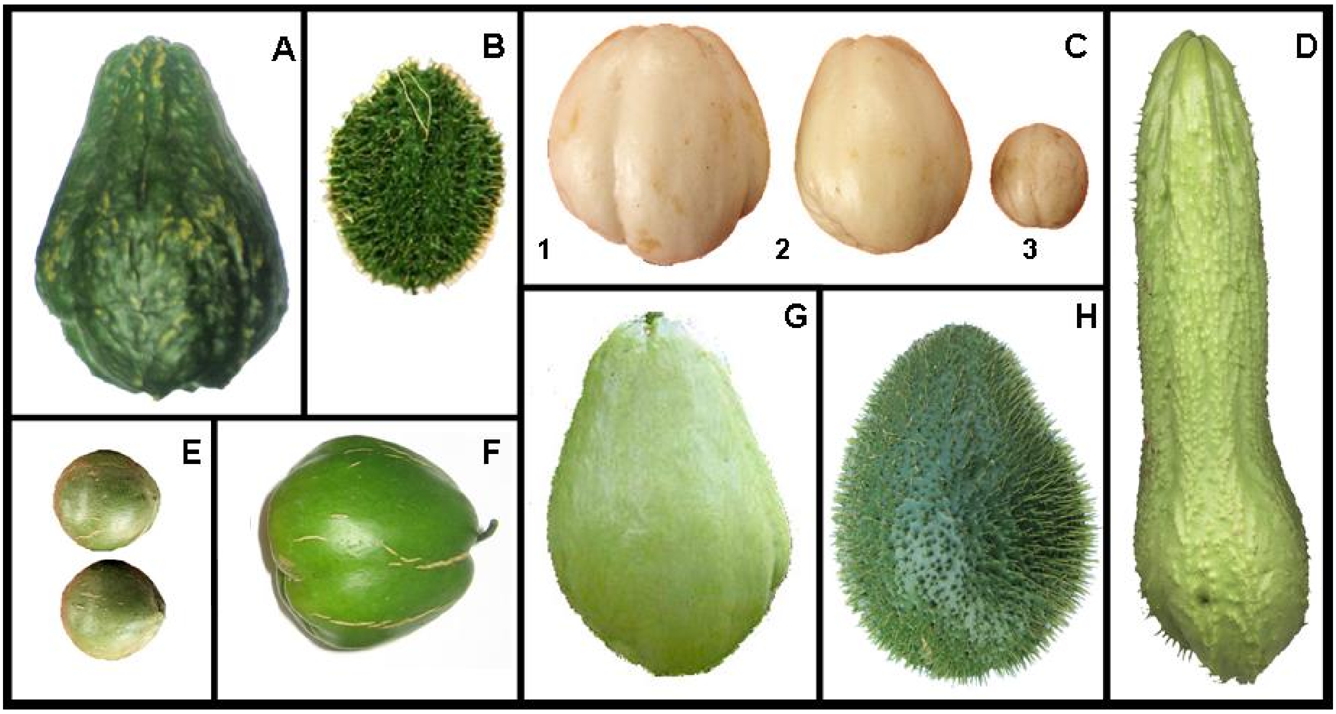

Fig. 1 Botanical varieties of *Sechium edule* (Jacq.) Sw. *nigrum xalapensis* (xalapa black) (**A**), *amarus silvestrys* (bitter wild) (**B**), *albus levis* (smooth yellow) (**C1**), *albus dulcis* (cambray) (**C2**), *albus minor* (castilla white) (**C3**), *nigrum maxima* (caldero for soup) (**D**), *nigrum minor* (castilla green) (**E**), *nigrum levis* (castilla black) (**F**), *virens levis* (smooth green) (**G**), *nigrum spinosum* (prickly green) (**H**). (unpublished)

tion between anthesis of the pistillated flower and staminated flower that provoke hybridization among the different types of chayote (Gamboa 2005). The confusion with respect to the types used by Lira *et al*. (1999) merited genetic considerations since the existence of chromosomal variation in cultivated plants with wide interval of morphological variation is indicative of domestication levels rather than of speciation (Harlan 1986). For instance *Vicia faba* L., so far, is only known in its cultivated form. The nearest wild relative seemed to be *Vicia narbonensis* L. but in addition to some morphological differences the cultivar with 12 chromosomes and a high amount of DNA is genetically strictly separated from the wild species containing 14 chromosomes (Hopf 1986). Also cytogenetic, biological, cladistic and morphological studies shown that "hill" sweet potato (*Dioscorea remotiflora*) and *D. remotiflora* var. 'Maculata' are two different species. The difference in the chromosomal numbers observed among these varieties, seem to be the evolution of *D. remotiflora* var. 'Maculata' under mountainous conditions (López 1999).

Jackson (1996) associates foliar polymorphism (common trait in *S. edule*) with certain chromosomal instability, the result of infraspecific hybridization, since their descendants are fertile and inherit various adaptive characteristics expanding variation patterns. Based on a morphostructural, biochemical, physiological, and genetic analysis, Cadena-Iñiguez (2005) proposed an arrangement of the infraspecific *S. edule* complex under a classification system into ten varietal groups, following the rules discussed for this purpose by Stace (1986); in this way he facilitated the identity of the biologic types, their conservation and use of described new qualities and different from the traditional ones for the genus (**Fig. 1**).

CROPPING SYSTEMS

Traditionally chayote has been cultivated in backyards. The first formal orchards in Mexico date back to approximately 95 years and their cultivation was carried out in soil similar to that of pumpkin, without using supporting structures for the plant with climbing habits. In this system the commercial product was physiologically ripe chayote (35 days after anthesis) (Stephens 1994), however, the increase in national and international demand brought about changes in consumer preference towards fruits at horticultural maturity (18 ± 2 days after anthesis); this led to the use of the *tapanco*. The *tapanco* is a structure of poles (wood, concrete or metal) of 2.2 m in height and wire in a reticulate form which has served as horizontal support to the vines in order to reduce mechanical damages and to improve fruit health and quality (Dzib *et al*. 1993).

Cultural practices

The system of plantation begins with sowing two physiologically ripe fruits (showing striae on the epidermis). The known kinds of sowing are "arrimo" (pile), "hoyo" (hole) and "hilera" (row)". The first consists in forming mounds of loosened soil where two fruits are deposited up to two thirds of their size and guided with tutors towards the *tapanco*. The second way is to hoe 0.4 x 0.4 x 0.4 m holes in the soil, following an arrangement of plantation in square, where two fruits are placed on a mound formed with the soil taken from the hole and guiding the plant to the *tapanco*. The last way is to form rows that require mechanical soil preparation; the fruit is sown at the required distance at the back of the row (Cadena-Iñiguez 2005). The density of plantation varies according to the type of vegetation prevailing in the crop region. In mountain cloud forest (1000-1450 m) the density is 100-130 plants ha^{-1}; for areas limited to vegetation of middle perennial and sub-perennial forest (500-950 m), from 400-600 plants; whereas in low deciduous forest (200-350 m) densities from 1100 to 1300 plants ha^{-1} are reached. This variation is based on the fact that the sites with less altitude present lower relative humidity, higher temperature and irradiance, which limit the growth of the vines, making it necessary to increase the number of plants in order to obtain a total cover of the *tapanco* and thus achieve the production. The commercial yields fluctuate between 54 ton ha^{-1}, for crops with traditional management and up to 136.3 ton ha^{-1} for those that follow technological guidelines (Cadena-Iñiguez *et al*. 2005). Gamboa (2005) reported yields up to 205 ton ha^{-1} under experimental conditions in Costa Rica. The commercial duration of the plant is one year and it produces during six or seven months; in this period it is recommended to carry out pruning, which results

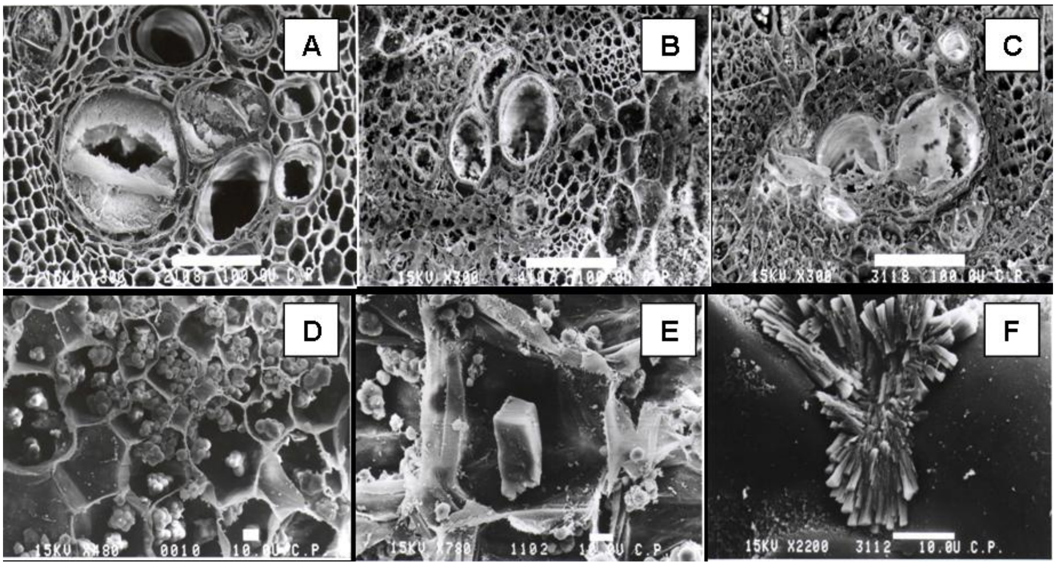

Fig. 2 Xylem cross section of the stem of *S. edule* plants var. *virens levis*, developed in calcareous soil. Obstructed xylem (**A-C**), sphero-crystals and cubic crystal (**D, E**), styloid breaking epidermal cells of adaxial leaf surface (**F**). Micrographs of scanning electron microscope at 300X, 300X, 300X, 480X, 780X, 2200X respectively. (Source: Cadena-Iñiguez *et al.* (2005) *Revista Chapingo Serie Horticultura* **11**, 309-316, with kind permission from the Editor and Chief).

in higher productivity and plant rejuvenation (Cadena-Iñiguez *et al*. 2005). In ecological terms, chayote crop without soil removal, use of mattock, or herbicides has represented an ecological option for the management of hillsides in areas of mountain cloud forest. Its management on *tapancos* forms a vegetal canopy, which absorbs the impact of rainfall, moderates the formation of water currents washing the hillside soils; besides, it continuously contributes biomass by shedding leaves and pruning of vines. Due to the fact that the water content in the plant is close to 95% (Lira-Saade 1996), supplementary irrigation is required weekly (Nuñez 1994), in quantities of 60-150 L plant^{-1} when the crop gets established in December-January and flowering appears in five months, and no additional irrigation is required when the plantations are established between June and September because of the rain season, the flowering appears 2 or 2.5 months after sowing, owing to the photoperiod (12 h). These factors have conferred to chayote certain agro-ecological adaptability motivating partial or total restructuring of areas producing potato, tobacco, maize, coffee, mango, and citrus in Mexico (Cadena-Iñiguez *et al.* 2001).

Commercial production in any of the cycles depends to a great extent on insect pollination activity since their reproduction is crossed. For *S. edule* the main pollinator reported is *Trigona* sp., and as secondary pollinators *Bombus mexicanus*, *Aphis mellifera*, *Polybia* sp., *Stelopolybia* sp., *Synoeca surianama* L., *Parachartegus* sp., *Augochloropsis* sp., *Lasioglossum* sp., and *Neocorynura* sp. (Wille *et al.* 1983; Bermejo and León 1994).

Nutrition

In commercial plantations of Mexico established in acid to slightly acid soils, monthly fertilizations of macronutrients are carried out with NPK relations from N170 P46 K180, to N220 P46 K240. In Costa Rica, Pacheco *et al*. (1990) report applications from N200-300 to N1257 kg ha^{-1}, but they favor the incidence of *Mycovellosiella cucurbiticola*. In slightly alkaline to highly alkaline soils in Mexico with presence of Ca (37-53 mg kg^{-1}), Mg (3-6 mg kg^{-1}), HCO_3 (≥3.9 meq L^{-1}), and pH with values between 7.3 and 7.9, the species presents physiological stress, generating large quantities of crystals, which obstruct xylem bundles (**Fig. 2**), chlorophyll is reduced provoking color loss of commercial fruit, which turns from light green to white. In order to mitigate this problem, Cadena-Iñiguez *et al*. (2005) recommend the use of a nutritional mixture of N170 P46 K220 Fe30 Mn30 Zn30 in sulfated sources (SO_4^{-2}), besides 75 kg ha^{-1} of agricultural sulphur as soil improvement, as well as inoculation at the moment of sowing with 40 g of *Glomus intraradices* and 40 g of *Azospirillum brasilense*, showing a reduction between 78 and 85% of crystals and return of the green fruit color.

Application of organic manure (of bovine or hen origin) is important to sustain the production, the recommended quantity being 70 kg plant^{-1}, which contribute between 140 and 175 units of nitrogen. Though the abuse of this manure favors fruit growth in less time and increases the intensity of green color, it makes them highly susceptible to mechanical damage. Another effect of the abuse is rotting of the plant roots since the dung utilized as manure, generally contains eggs or larvae of *Phyllophaga* sp. and *Diabrotica* sp. which attack the roots and facilitate the infection by *Erwinia* sp. and *Phythophtora capsici* quickly causing plant death.

Propagation

The most common type of propagation is via sexual using the physiologically mature fruit that contains only one endocarpel seed germinating inside the fruit (viviparous), when this is still adhered to the mother plant. Fruit maturity is reached at 35 days after anthesis (Stephens 1994), and the sign is the appearance of numerous striae on the epidermis. An adaptive function in *S. edule* fruit, favoring its survival, lies in the quality of the pericarp, which does not decompose as most of the fleshy and soft fruits do. Ethylene production by the fruit is close to 5 ng kg^{-1}s^{-1} (Cadena-Iñiguez *et al*. 2006), considered very low, and not enough to generate the decomposition of the pericarp, neither the fermentation, given the low concentration of sugars and the high water content (Flores 1989). In 1763, Jacquin, quoted by Lira-Saade (1996), besides Longo (1907) and Marola (1949) quoted by Flores (1989), considered relevant that the beginning of seed germination takes place, the fruit being closely adhered to the mother plant so that water and nutrients of the pericarp are transported to the new seedling granting independence of climate and soil until it can establish on its own; otherwise, being a large and heavy fruit, it would get spoiled at falling to the ground and would provoke the death of the seed.

Based on a structural analysis of fruit and seed, Orea and Engleman (1983) determined that the testa cells do not become lignified, which together with the fusion of the testa with the pericarp promotes viviparous germination. The same authors agree with the results of Longo (1907), who had concluded that the testa function was not seed protection, but, together with cotyledons and the pericarp, the storage of nutrients, to be utilized by the embryo during germination. Flores (1989) considers that the success of *S. edule* survival is based on five factors, which promote endocarpal germination: 1) quick disappearance of the germination-inhibiting substance, which coincides with the physiological maturing of the embryo; 2) water abundance in the

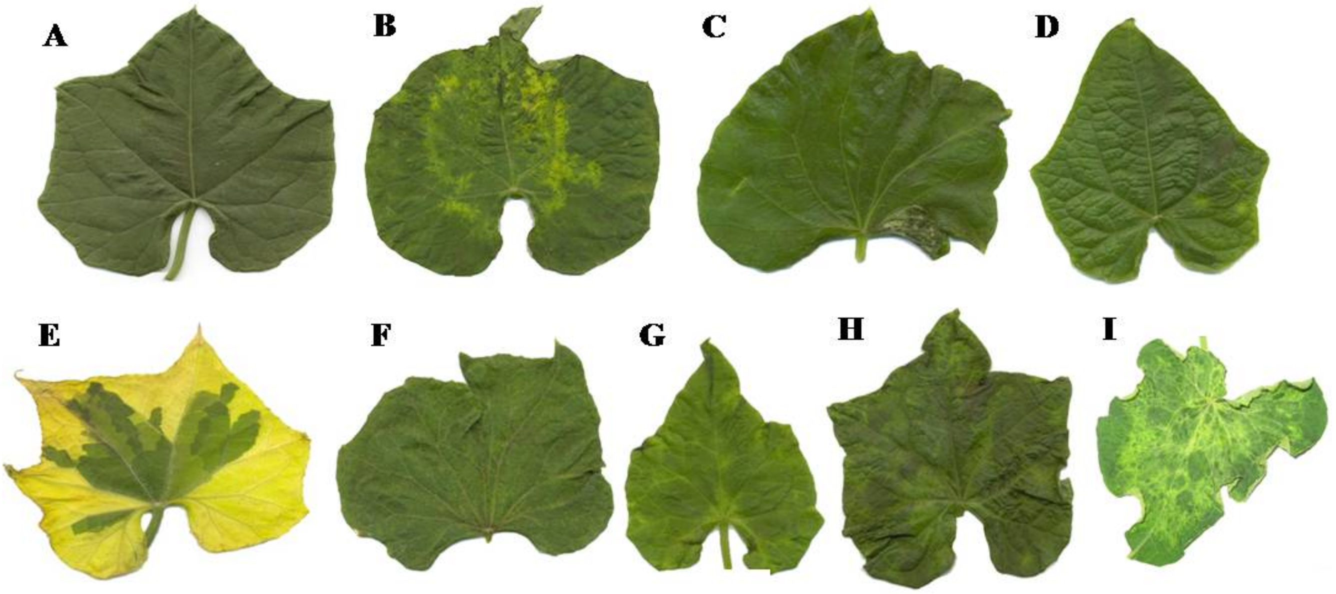

Fig. 3 Viral infection symptoms in *Sechium edule* leaves. Healthy leaf (**A**), leaves with mosaic symptoms (**B-I**) (unpublished).

pericarp, which is transported to the embryo; 3) the presence of nutritive substances in the fruit and cotyledon starch, which is hydrolyzed and utilized in embryo growth; 4) absorbent action of cotyledons and 5) the structure of the fruit.

It is worth mentioning that *S. edule* fruit has stomata and chlorophylls *a* and *b*, and carotenoids in yellow fruits that allow for carrying out gas exchange and photosynthesis, being an adaptive advantage for maintaining a balance of energy use and avoiding to debilitate the nutritional reservoir of the pericarp itself during germination and independence of the seedling. With relation to asexual propagation, *in vitro* culture (Abdelnour-Esquivel *et al*. 2002) and rooting of terminal cuttings of vines have been reported in a time not longer than 32 days. The successful evidence of propagation *in vitro* showed that treatment under osmotic pressure of 6% sucrose and at a temperature of 18°C caused the least damage to explants and no morphological alterations (Alvarenga-Venutolo and Venutolo-SA 1990) although this practice is not conducted commercially. The micropropagation for *Sechium edule* has been reported in vegetative shoots on MS medium with 0.1 mg L^{-1} BA or without plant growth regulators (Somarribas *et al*. 1991; Abdelnour *et al*. 2002). Also micropropagation of hypocotyls has been successfully achieved on MS medium supplemented with 0.1 mg L^{-1} IAA and 1 mg L^{-1} BA (Wang *et al*. 1997). GISeM is trying to propagate different tissues through the response by direct and indirect organogenesis, also indirect somatic embryogenesis, using several growth regulators.

Pests and diseases

The *S. edule* crop is attacked by different pathogenic fungi among which *Ascochyta phaseolorum*, and several species of *Fusarium*, *Macrophomina*, and *Colletotrichum* are outstanding. Basic studies on the most important diseases (*Ascochyta phaseolorum*, *Mycovellosiella cucurbiticola*, *Fusarium oxysporum* and complexes of these and other species), particularly those which attack the fruit and which cause 35 to 40% of the rejects in commercial production (Bermejo and León 1994) were carried out. Also *Pseudomonas syringae* pv. *Lachrymans* was consistently isolated from lesions on diseased chayote; leaves collected in Porto Rico, and isolates were also obtained from honeydew melons, numerous with irregular tan to brown water-soaked lesions. Pathogenicity was confirmed (Cortes-Monllor and Rodríguez-Marcano 1991), and blister *Mycovellosiella* sp. was identified as a causal agent of this disease in Costa Rica. The symptoms were reproduced by inoculation of *S. edule* fruit using a spore suspension (Vargas 1988).

In the very hot periods of the year mites attack on the underside of the leaf and occasionally, the young (tender) fruits; the main species found were *Tetranychus urticae*, which accounted for 80% of the total population, and *Paraponychus corderoi* and *Eutetranychus banksi*, each of which accounted for 10% of the total population (Vargas 1988). The cerambycid *Adetus fuscoapicalis* and the gastropod *Macrochlamys* sp. are also pests of economic importance (Lamonica-Imenes *et al*. 1989).

A potential threat for the chayote crop is infection by virus; for Costa Rica the presence of *Tymovirus* (Bernal *et al*. 2000) and *Begomovirus* for India (Mandal *et al*. 2004) has been reported. In Mexico GISeM had been detected in commercial plantations, with different symptoms of viral infection in plant leaves (**Fig. 3**), which so far have not affected their development and productivity, however, the identification of the causal agent is under study.

GENETIC IMPROVEMENT AND VARIETIES

S. edule presents a wide range of biological types; *nigrum spinosum*, *nigrum xalapensis*, and *virens levis* (**Fig. 1**) are commercially cultivated, the latter, known as smooth green chayote, is the only one traded on the international market. Generally, an infraspecific variant within the same type, obtained by interchange of fruits among producers and localities, is utilized as seed source. This implies several problems: it is unknown whether the seed source is a type with predominant and stable forms, or whether it is a product of hybridization with high percentage of segregation. This has caused economic failures due to low quality of the final product since it does not fulfill the prospects of the market, especially with respect to form, size, and color.

Another problem is the dissemination of pathogens such as viruses (*Tymovirus*, *Begomovirus*) (Bernal *et al*. 2000; Mandal *et al*. 2004), fungi of the genera *Mycovellosiella*, *Geotricum*, *Phytophtora*, *Colletotrichum* (Vasquez *et al*. 1986), bacteria (*Erwinia* sp.), and nematodes (*Meloidogyne incognita* and *Helicotylenchus* sp.) (Rivera and Brenes 1996).

With respect to the advances of genetic improvement, Gamboa (2005) mentions the existence of clones in Costa Rica and warns that the use of these materials has diminished in the medium term the profitability of the crop, due to uniformity of the genetic material, which has provoked genetic erosion, that is why it is suggested to be avoided (Engels 1983). Genetic improvement of chayote has been used by producers anciently in an informal way; nevertheless, Gamboa and Ramos (1989) report that in 1989 in Costa Rica an export program of genetic improvement was initiated in Valle de Ujarrás, where the characteristics to be improved were: organoleptic, resistance to pests and diseases, archetype, and yield components (number and length of stems per plant, internode length, quality, weight and number of fruits per vine). This program was carried out in different phases, beginning with collection and selection of plants, establishment of a germplasm bank, improving of the methodology to generate clones, obtaining of synthetic varieties, pure lines, hybrids, and their production in a commercial way. Two hundred and fifty plants of commercial orchards were selected, called "mother plants", 34 of which were chosen for asexual propagation through cuttings; subsequently, they were sown in the same valley to be characterized and selected. Asexual reproduction was a basic tool in the program due to allowing for the conservation of the collections and obtaining of clones (Gamboa 2005). The experimentally outstanding clones were: EY13, SA15, EY17, SA21, UJ27, UJ28, and UJ29; the experimentally obtained yields fluctuated between 56.4 and 202.5 ton ha^{-1}, whereas the outstanding synthetic varieties were: VS17, VS28, and VS29, characterized by having good adaptability, yield, and in some cases, excellent fruit quality. The lines were obtained from two self-fertilizations, without reporting hybrids. Based on the experience of previous improvement, countries like Honduras, Nicaragua, and Panama are receiving biological material from Costa Rica in order to formally enter the international market (Brenes-Hine 2002). In Mexico, the GISeM has been developing cultivars using the method of stratified mass-visual selection for different agro-climatic conditions.

Conservation and greater knowledge of *S. edule* germplasm, expressed in its infraspecific variation, represents the main reservoir for future works of genetic improvement. In the decade of the eighties germplasm banks were created in different countries: Mexico, Nepal, India, and Costa Rica (Ortega-Paczka *et al.* 1998). Regrettably, problems like root rotting, pest attacks, cold damage, and occasionally, damage by cattle, caused the gradual loss of this material between 1982 and 1990 (Brenes-Hine 2002). It is well-known that only in the hills of Nepal, India, there is *in situ* germplasm bank of chayotes (Baral *et al.* 1994; Sharma *et al.* 1995). Two other institutions caring for collections of *S. edule* are the Instituto Superior de Ciencias Agropecuarias of Nicaragua (Experimental Center Blue Fields) and the Centro Nacional de Pesquisas de Hortalizas (EMBRAPA, Brazil); in Costa Rica, Gamboa (2005) mentions that in 1992 a germplasm bank for *S. edule* was created, however, there are no reports on the current state of these collections.

One of the most important topics of the genetic improvement is cytology. Studies by Sanjappa (1979), show that the size of the chromosomes for *S. edule* varies from 0.7 to 1.9 μm and secondary constrictions are present in two chromosomes. The number of chromosomes according to de Donato and Cequea (1994) is 2n=28, nevertheless Sigiura (1938), Sobti and Singh (1961) quoted by de Donato and Cequea report 2n=24. This discrepancy has been attributed to the translocations of meroaneuploids, which consist in the formation of one chromosome from the fusion of two. Because of this in June 2005, GISeM created the Banco Nacional de Germoplasma (National Germplasm Bank) of *S. edule*, with accessions coming from the center and southeast of Mexico, Guatemala, and Costa Rica, associating them in ten varietal groups (**Fig. 1**). One of the objectives of this effort is to identify the origin of the chromosomal variation through karyotypic and molecular studies of the accessions.

ECOPHYSIOLOGY

Under natural conditions of mountain cloud forest, *S. edule* develops as a climbing, basically orthotropic plant, whereas under crop conditions its growth is induced to plagiotropic position, remaining exposed to higher irradiance and environmental temperature. Due to the increase in demand, crop areas have been extended, the agroclimatic limits for its development, which has provoked reductions in yields and low fruit quality.

Climate

The climate as primary element acts as a modifier of other elements of the environment, such as vegetation and soil (Soto and Gómez 1994). Under wild conditions, *S. edule* is located in zones with climates of type Af(m), Am, classified as humid, and within these the semi-hot types (Ac(m) a(i)g). Altitudes go from 800 to 1500 m, with high relative humidity (80-85%), annual mean precipitation between 1500 and 2000 mm, and temperatures between 20 and 25°C (Lira-Saade 1996; Cadena-Iñiguez 2005). Under crop conditions its distribution is more extensive, since it is commercially located from 2500 m for var. *n. spinosum* in high valleys to altitudes lower than 100 m in regions of high relative humidity for var. *virens levis*.

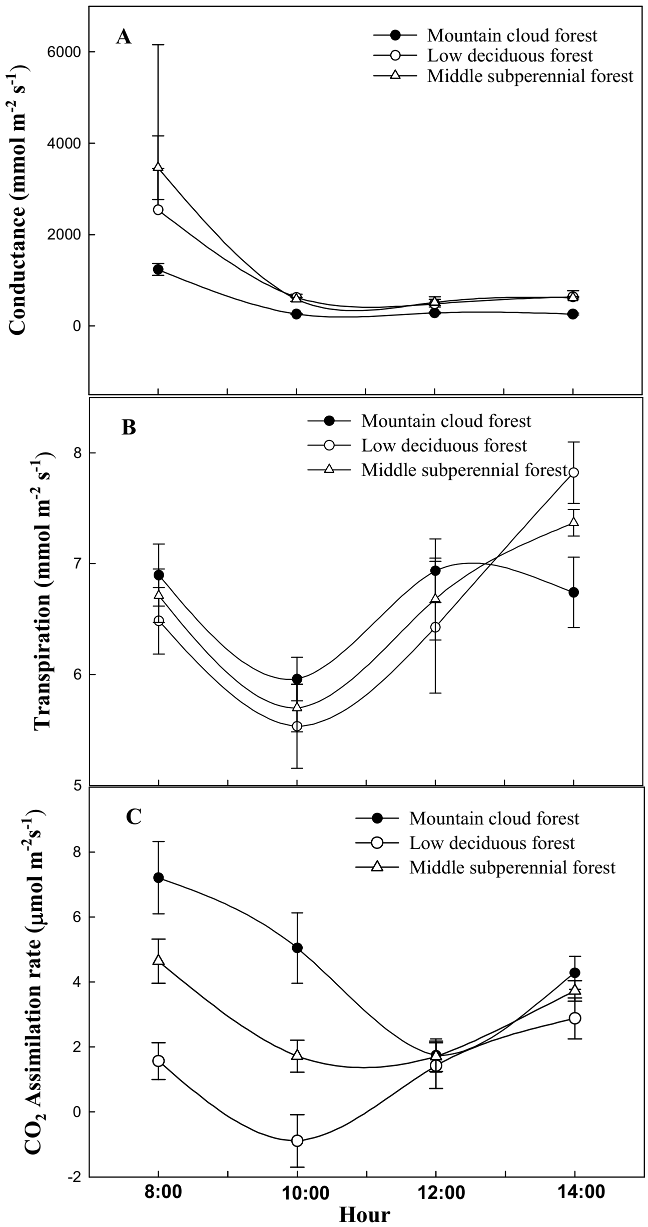

Fig. 4 Day pattern of gas exchange of *S. edule* plants var. *virens levis* under field conditions in three agroclimatic environments. Stomatal conductance (**A**), transpiration (**B**), CO_2 assimilation rate (**C**). The values are the product of 10 measurements for each hour ± standard error. (unpublished).

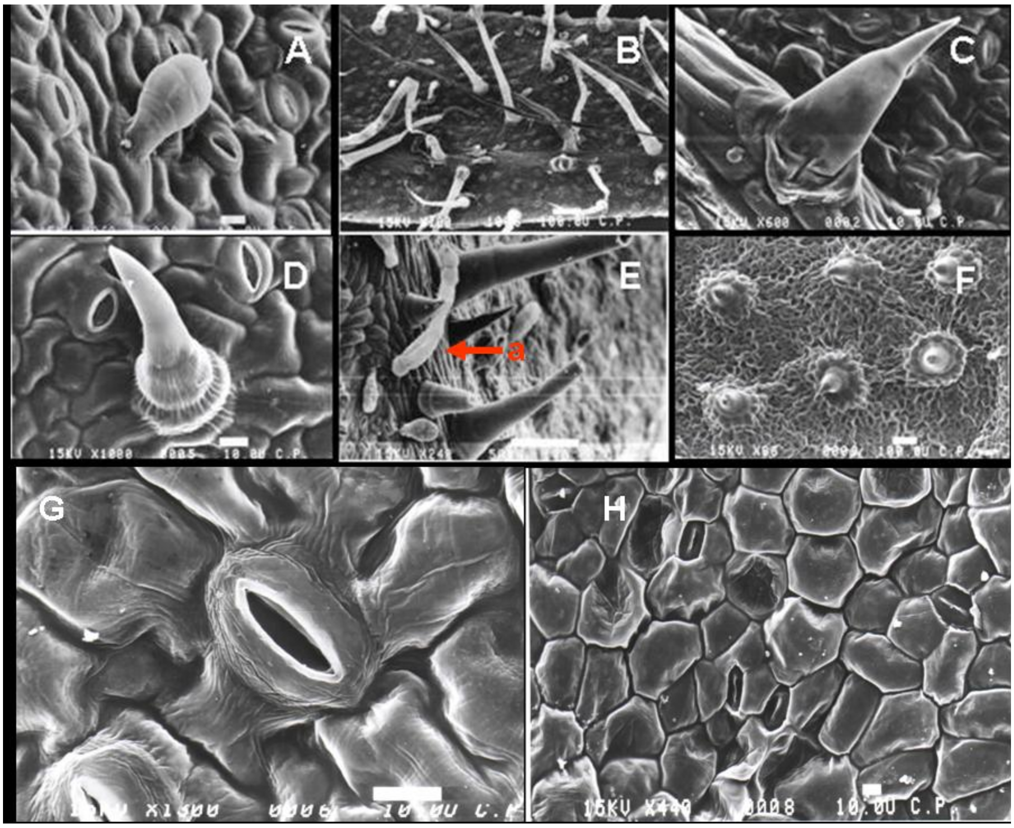

Fig. 5 Types of trichomes and stoma observed on leaves of cultivated and wild *S. edule*. Abaxial surface: Glandular (**A**), septate (**B**), strigose (**C**), solitary (**D**), moniliform (**Ea**). Adaxial surface: cystolithic (**F**), anomocytic stoma on abaxial surface (**G**), adaxial surface (**H**). Micrographs of scanning electron microscope. 866X, 100X, 600X, 1000X, 240X, 86X, 1300X, and 440X respectively. (from Cadena-Iñiguez 2005)

Soils

The soils must be well drained, rich in humus, with acid to slightly acid pH (4.5 to 6.5) (Lira-Saade 1996), where Ca^{2+} and Mg^{2+} availability is relatively low, and that of Fe^{2+}, Mn^{2+}, and Zn^{2+} is high. Commercial plantations, which have been established in calcareous and slightly saline soils (pH: 7.0-7.9) with the presence of Na^+, Cl^-, SO_4^{2-}, HCO_3^-, and high Ca^{2+} and Mg^{2+} content, reduce crop productivity and fruit quality (Cadena-Iñiguez *et al*. 2005).

Water relations and gas exchange

One of the main limiting factors for the productivity of a species is low water availability. *S. edule* is no exception; it has been deemed that one hectare of crop requires approximately 936,000-3,750,000 L of water per cycle (Dzib *et al*. 1993), so that the conditions of extreme drought cause plant death. The day pattern of gas exchange and water relations is considerably affected when the crop is outside its original habitat, probably due to changes in temperature, incidence of solar radiation, relative humidity, and nutritional soil conditions related to the agroclimatic region. **Fig. 4** shows the changes in the day pattern of gas exchange of *S. edule* var. *virens levis* under field conditions in the three types of vegetation, where it is extensively cultivated, considering mountain cloud forest as original environment. In this study, plants have been detected to show temporary withering at noon, when temperature and incidence of solar radiation are higher. When water demand by transpiration increases, potential of water and plant turgidity diminish at the time osmotic potential increases, activating the partial close of stomata (**Fig. 5**) and avoiding (water) loss by transpiration and CO_2 assimilation (Cadena-Iñiguez *et al*. 2001). Also changes in the mineral concentration of xylem sap, like K^+ and Ca^{2+}, are registered, elements of higher concentration, which have a constant relation during the day pattern from 3:1 until 6:1. These changes influence pH so that the highest acidity is related to stomatal opening, to a higher K^+ concentration, and to lower environmental (24-28°C) and leaf temperature (20-26°C). On the other hand, alkaline values of pH are related to higher Ca^{2+} concentration, stomatal closure, environmental and leaf temperature above 38 and 30°C, respectively.

Recent studies have demonstrated that the efficiency in water use is higher when there is greater variation and frequency of trichomes in the leaf than when there is only one type of trichome. Several studies show that trichome density (number of urticant trichomes per unit leaf area) of *Wigandia urens* (Ruiz & Pavon) Kunth (Hydrophyllaceae) and *Tectona grandis* L. was higher during hydric stress rather than when is not present, because less diversity and scanty distribution of trichomes provoked water loss (Pérez-Estrada *et al*. 2000). Then the increase of trichomes reduces the heat load, maintaining leaf temperatures and reducing the transpiration rate by reflecting excess visible and infrared light, creating an energy balance in the leaf, and increasing the resistance of the border layer, forming a humid layer (Bandyopadhyay *et al*. 2004). In chayote varieties, the highest frequency and variation of trichomes is observed on the abaxial surface, glandular trichomes being most abundant, followed by the solitary and septate ones (**Fig. 5**). Generally, the varieties of yellow fruits (var. *albus levis*, *a. dulcis*, *a. minor*) have more trichomes, while the green fruits show lower frequency, mainly var. *nigrum xalapensis* and *virens levis* (Cadena-Iñiguez 2005).

POSTHARVEST MANAGEMENT

Except for wild chayotes characterized by their bitter flavor, the rest of the chayotes are cultivated commercially or promoted in backyards for self-consumption. Costa Rica is the first world-wide exporter of chayote, it produces an area not larger than 500 ha, exporting 92% of its volume (Brenes-Hine 2002). Mexico, the second world-wide producer, grows approximately 3634 ha (Cadena-Iñiguez 2005). Both countries produce the var. *virens levis* although with different shapes, Costa Rica fruits are obovoid while Mexican fruits are piriform (**Fig. 6**). The greatest challenge, however, is not the increase of the production surface, but improving the production process from harvest to packing and distribution. The State of California, United States is one of the biggest markets of chayote, where it is very appreciated by the Latin and Asiatic communities, getting prices up to $US

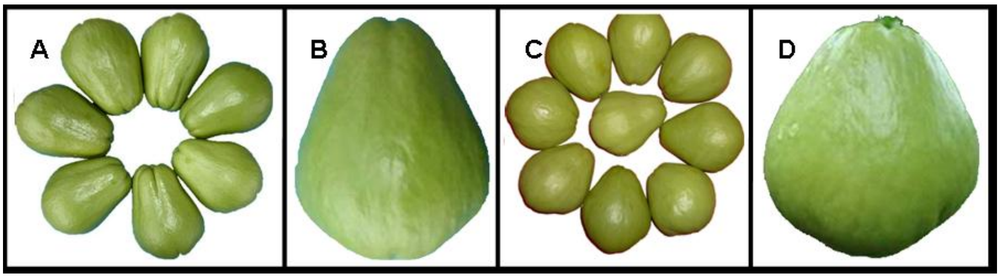

Fig. 6 Morphological variation of commercial *Sechium edule var. virens levis* which are exported to North American markets. Pyriform type from Mexico (**A, B**), obovoid type from Costa Rica (**C, D**). The fruits come from commercial orchards. (unpublished).

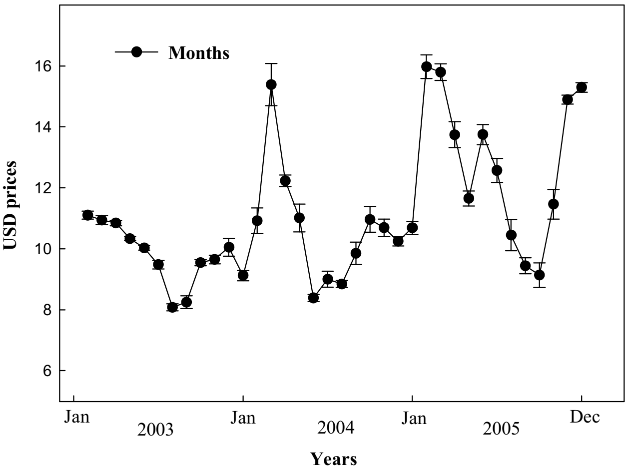

Fig. 7 Average starting price for the years 2003, 2004, 2005 to the intermediate consumer for 18.1 kg (40 pound) box of chayote on the market of Los Angeles, Ca., USA, (Source: Continental Growers Co.) (with kind permission).

16.0 per 18.1 kg (40 pounds box) in winter, due to climatic factors in the production areas (**Fig. 7**). Regarding this, a reliable postharvest management is fundamental, guaranteeing fruit health and quality. Therefore in the last years some techniques that reduce damage by friction and seed germination have been implemented, which presents new alternatives for its marketing.

Harvest Index

Some basic requirements, established to determine the quality of smooth green chayote fruits, focus on coloring (light green), size (0.2-0.5 kg in weight and 12-16 cm long), as well as on health and defects (Anonymous 2003). Nevertheless, there are few references which define the most adequate harvest index. Cadena-Iñiguez *et al*. (2006) mention that the chayote fruits may be harvested at 18 ± 2 days after anthesis, Piatto (2002) states that the harvest is carried out 35 days after pollination; others, like Aung *et al*. (1996) point out that the harvest is carried out when the fruit reaches a weight between 250-400 g. These apparent discrepancies become clear for two reasons, the first is considering that age and size of the fruit utilized as seed will generally determine size and time of growth and development of the fruits of this plant and the second because the degree of maturity that the market demands.

The chayote fruit is harvested at horticultural maturity, a state when it has not yet reached total development, but has the optimal characteristics for consumption. Respiration rate of chayote fruits is between 3-5 mg CO_2 kg^{-1} h^{-1} at environmental temperature (Cadena-Iñiguez *et al*. 2006). Aung *et al*. (1992) reported respiration values at 25°C, after refrigerated storage for twelve days between 10.8 and 13.5 mg CO_2 kg^{-1} h^{-1}. Ethylene production is very low (up to 18 µg C_2H_4 kg^{-1} h^{-1}), tissue damage being reported because of the presence of this hormone in concentrations of 1 mg kg^{-1} (Yudin and Schlub 1998), so that among vegetables chayote is classified as one of those of low CO_2 and ethylene production.

Selection and packing

It is recommendable to harvest the fruit early in the morning, since due to the crop conditions the tissue is turgid and at low temperature, that is why the use of pre-cooling is not a common practice. Valverde *et al*. (1989) report that precooling of the fruits with water at 0°C before storing at 12-14°C does not contribute to reduce their weight loss, however, this study does not mention harvest conditions. After harvest, the fruits are selected considering characteristics such as form (obovoid or pyriform), color (olive green), appearance (smooth, without spines), and health (Anonymous 2003).

The fruits are packed in individual perforated polyethylene bags, with the purpose to avoid accumulation of water vapor, product of transpiration. The commercial presentation of transport is in boxes of 24 and 60 pieces. The most commercial calibers are of 200 and 220 g per fruit (Anonymous 2003). The fruits can be transported overland or by sea in refrigerated containers of 20 ton of capacity, containing 60-62 thousand fruits, respectively; transport conditions must be around 11°C (52°F) and 80-85% RH.

Storage

Viviparism or seed germination appears at environmental temperature after one week of storage, while at refrigeration temperature it appears before three weeks; this problem is so common that even when the fruits are attacked by pathogens or suffer cold damage, viviparism appears invariably. Due to the fact that the seed is soft and has high moisture content provided by the fruit, besides not having a period of dormancy, seed germination is imminent (Orea and Engleman 1983; Valverde *et al*. 1986). This phenomenon together with weight loss and incidence of diseases during transport and storage constitute the main problems reducing quality and commercial value of postharvest fruits.

Viviparity of *S. edule* was reduced with injections of prohexadione (1 mM) in the fruit cavity, a growth regulator which inhibits the synthesis of gibberellins, being more effective in semi-mature fruits (250 g) and delaying the emergence in well-developed fruits (400 g) (Aung *et al*. 2004); however, this technique, though effective, represents serious operating disadvantages in commercial shipments (Aung *et al*. 1996).

On the other hand, as the endogenous action of ethylene during the germination process has been proved in some seeds, the application of antagonists to the action of this plant hormone has given promising results for the inhibition of germination (Zehhar *et al*. 2002). One of the compounds, which have proved to be effective in inhibiting ethylene action, is 1-methylcyclopropane (1-MCP), competitor of the recipient site of ethylene, which has been applied to numerous horticultural products (Blankenship and Dole 2003); in chayote different doses of 1-MCP (300, 600, and 900 nL L^{-1}) were applied to fruits stored for 28 days at 10°C plus 6 days at environmental temperature; the results showed that the dose of 300 nL L^{-1} reduced germination by 5% compared to 50% of the control fruits (Cadena-Iñiguez *et al*. 2006).

The optimal storage temperature fluctuates between 10 and 15°C, while higher temperatures provoke early seed

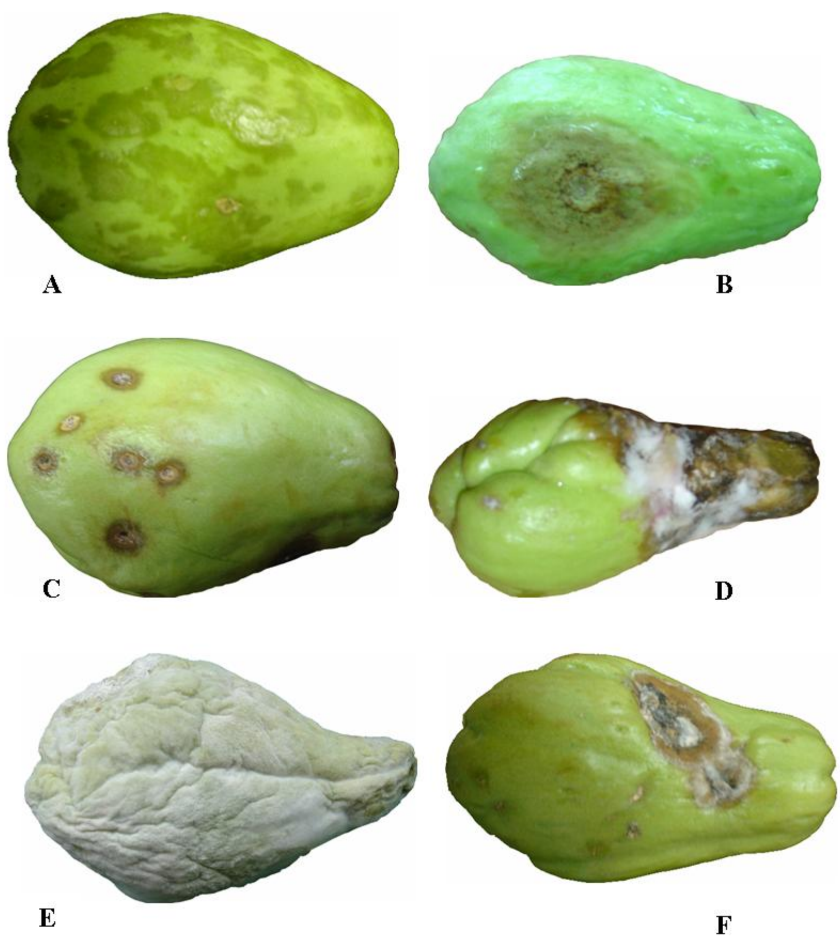

Fig. 8 Symptoms of postharvest diseases in chayote (*S. edule*) fruits. Bladder or blister (*Colleotrichum gloeosporioides*) (**A**); Anthracnose (advanced symptom) (*Colletotrichum orbiculare*) (**B**); Anthracnose or freckles (initial symptom) (*Colleotrichum orbiculare*) (**C**); Reddish-purple mould, (*Fusarium oxysporum*) (**D**); White mould (*Phytophthora capsici*) (**E**); Acid rot (*Geotrichum* sp.) (**F**). (from Juárez 2006, with kind permission)

germination, and temperatures below 7°C produce cold damage, showing as marks sunken in the epidermis and dark brown spots, which are more evident at environmental temperature. Another problem is the damage caused by scratches; therefore it is a common practice to put the fruits into bags after selection, though the application of wax has also proved to be effective in avoiding these damages and improving fruit appearance (Cadena-Iñiguez *et al*. 2006).

Storage in modified atmospheres is an effective alternative due to the reduction of weight loss by 30% at 25°C, and around 40% at 10°C after five weeks of storage, when the fruits were kept in polyvinyl chloride film (PVC) (Aung *et al*. 1996). Likewise, due to the low respiratory rate of chayote, it has been reported that ethanol and acetaldehyde production does not present significant increases during storage (10-12°C) up to four weeks. Consequently, technologies such as low temperature, modified atmospheres, and the use of ethylene action inhibitors are good alternatives to prolong shelf life, conserving the characteristics of fruit quality.

Postharvest diseases

One of the main causes of postharvest losses is the incidence of diseases, *Ascochyta phaseolorum*, *Macrophomina* sp., *Colletotrichum* sp., *Fusarium* sp. and *Mycovellosiella cucurbiticola*, *Phoma cucurbitacearum* among others (Saenz and Valverde 1986; Valverde *et al*. 1989) being causal agents for fruits originating from Costa Rica. In Mexico, however, the pathogens which have been identified during postharvest phase are *Colletotrichum gloeosporioides*, *C. orbiculare*, *Fusarium oxysporum*, *Phytophthora capsici*, and *Geotrichum* sp. (Juárez 2006).

The environmental conditions favoring *Colletotrichum gloeosporioides* are high temperature and relative humidity with an optimum of 24°C and 97% RH, wind and rain being common ways of dissemination. The infection begins by penetration of the fungus through the cutin by enzymatic action (cutinases) and remains latent until the fruit begins to mature and then quickly develops provoking the damage called bladder or blister (**Fig. 8A**). In the case of *C. orbiculare,* chayote fruits show, as the disease advances, circular dark spots, sunken, white in the center, with pink and dark acervuli (**Fig. 8B**) to be seen on any part of the fruit surface (Juárez 2006); this disease is also known as freckles (**Fig. 8C**). Some methods of control highlight the use of fungicides such as Tiabendazole (300 μg mL^{-1}) and allum (1%) (Valverde *et al*. 1989) however Alvarado *et al*. (1988) mention that there is certain physical control on the bladder at submitting the fruits to a temperature of 50°C.

Fusarium oxysporum attacks mainly the root, but the attack can be isolated in aerial parts like leaves and fruits. At postharvest it can be isolated from lesions with light rotting, presenting characteristic mycelium, spongy, of abundant white-reddish-purple color (**Fig. 8D**) (Juárez 2006).

The postharvest attack of *Phytophthora capsici* causes damage on the epidermis that appears as watery spots, which by the time grow and remain covered by the mycelium of the fungus, which may internally develop, provoking soft and sunken putrefaction (**Fig. 8E**). The infection by this fungus uses to be the result of infections caused in the field, not noticed during packing. The damage by *Geotrichum* sp. appears like a soft bitter or acid rot with superficial creamy white mycelium (**Fig. 8F**).

Though refrigerated transport, utilized as common practice in fruits, delays the development of these diseases, it does not avoid that they attack more severely at environmental temperature.

MEDICINAL AND NUTRACEUTIC USE

Chemical composition of chayote

Unlike other cucurbits, the fruit contains only a single large seed. The immature fruits can be eaten in salads and provide a good source of vitamin C. They can also be boiled, fried,

Table 1 Chemical composition of *Sechium edule* (Jacq.) Swartz. Data are reported per 100 g of dry matter.

COMPOSITION	Mature fruit	Seed	Leaf	Root
pH	6.5-6.7	-	-	-
Energy (Cal)	26-31	-	60.0	79.0
Moisture (%)	90-94.5	-	89.7	79.7
Protein (g)	0.9-1.1	5.5	4.0	2.0
Lipids (g)	0.1-0.3	-	0.4	0.2
Carbohidrates (g)	3.5-8.4	60.0	4.7	17.8
Fiber (g)	0.4-1.0	-	1.2	0.4
Ca^{2+}(μg)	12-19	-	58.0	7.0
P + (μg)	20-27	-	108.0	34.0
Fe^{2+} (μg)	0.4-0.8	-	2.5	0.8
N (μg)	4.85	-	-	-
Cu^{2+} (μg)	8.82	-	-	-
Zn^{+} (μg/ml)	8.4	-	-	-
Mn^{2+} (μg)	0.47	-	-	-
K^{+} (μg/ml)	38.0	-	-	-
Vitamin A (μg)	5.0	-	615.0	-
Tiamine (mg)	0.03	-	0.08	0.05
Riboflavin (mg)	0.04	-	0.18	0.03
Niacin (mg)	0.4-0.5	-	1.1	0.9
Ascorbic acid (mg)	11-20	-	16.0	19.0

(Source: Lira-Saade 1996, with kind permission).

Table 2 Relative content of cucurbitacins, total soluble solids and ascorbic acid in fruits of eight *S. edule* ecotypes (unpublished).

Variety	Cucurbitacins g 100 g^{-1}	TSC[1] °Brix[2]	Ascorbic acid[3] mg100 g^{-1}
virens levis	0.0116	5.14 ± 0.2	6.76 ± 0.16
nigrum xalapensis	0.0195	4.93 ± 0.2	6.53 ± 0.53
nigrum spinosum	0.0190	6.43 ± 0.3	4.95 ± 0.49
nigrum levis	0.0660	5.47 ± 0.2	6.65 ± 0.18
amarus silvestrys	0.1456	10.92 ± 0.3	3.99 ± 0.16
albus minor	0.0039	7.66 ± 0.7	7.82 ± 0.42
albus dulcis	0.0027	7.21 ± 0.9	7.42 ± 1.27
albus levis	0.0088	8.08 ± 0.6	7.75 ± 0.22

[1] Total Soluble Content[2]: mean of 196 determinations ± standard error
[3] Mean of 380 determinations ± standard error

steamed, or stuffed and baked. Young leaves and tendrils are also eaten, and seeds can be sautéed in butter as a delicacy. Lira-Saade (1996) reports the composition of different organs of *Sechium edule* (**Table 1**). The injection of an aqueous extract of chayote leaves caused a marked decrease of blood pressure in dogs and an increase of diuresis. The active chemical principle(s) causing these physiological changes are not known. Various members of the Cucurbitaceae produce bitter principles, cucurbitacins, in different plant organs; chayote may also contain these chemicals. Cadena-Iñiguez (2005) reports as part of fruit composition of eight *S. edule* varieties the total soluble solids, ascorbic acid, and cucurbitacins; the latter metabolite contains concentrations 100 times lower in the varieties of yellow fruits than in the wild ones, and 10 times lower than the cultivated varieties of green fruit (**Table 2**).

Thus, the predominant carbohydrate of the enlarged root of chayote was starch. They also found that in the actively growing distal 10-12 cm of tender apical shoots, 0.3% soluble sugars on a wet-weight basis, and 0.7% starch. The carbohydrate content presumably contributes to the taste and nutrition of the chayote sprouts, which are highly valued as a cooked delicacy and as a source of vegetable greens of inhabitants of tropical regions. Analysis of the chayote fruit flesh showed the following results: 33.3% soluble sugars on a wet-weight basis and 0.2% starch; in the seed, 4.2% soluble sugars and 1.9% starch. In the pulp, the sugars found were glucose and fructose, whereas in cotyledons saccharose and raffinose were found (Aung *et al.* 1992). At comparing the soluble sugar content of the organs, the whole fruit contained 15 times more soluble sugars than the storage roots and 25 times more soluble sugars than the apical shoots. In contrast, the starch content in the whole fruit was only 1/8 of the storage root. With respect to other chemical constituents, MacLeod (1990) found in the chayote fruit nearly 61 volatile components. Major components were octadeca-9,12 dienoic acid (16.4%), docosane (10.9%), oct-1-en-3-ol (10.4%) and (*Z*)hex-3-en-1-ol (10.1%), the latter two components contributing characteristic odor to the green fruit. Other previous phytochemical studies on *S. edule* fruits led to the isolation of sterols, nonphenolic alkaloids and saponins (Salama *et al.* 1986), whereas Siciliano *et al.* (2004) described the characterization of flavonoids in different parts of edible organs of *S. edule*. Eight flavonoids including three C-glycosyl and five *O*-glycosyl flavones were detected and quantified in roots, leaves, stems, and fruits of the plant. The aglycone moieties are represented by apigenin and luteolin, while the sugar units are glucose, apiose, and rhamnose. Their results indicated that the highest total amount of flavonoids was in the leaves (35 mg 10 g^{-1} of dried part), followed by roots (30.5 mg 10 g^{-1}), and finally stems (19.3 mg 10 g^{-1}).

The cucurbitacins are a group of bitter tasting, highly oxygenated, mainly tetracyclic, triterpenic plant substances derived from the cucurbitane skeleton [19-(10-9β)-abeo-10α-lanost-5-en]. They cannot be considered as steroidal since the methyl from carbon 10 has moved to carbon 9. The cucurbitacins are predominantly found in the Cucurbitaceae family but are also present in several other families of the plant kingdom. They are usually present in the plant as β-glucosides. These cannot be isolated if the species has the hydrolytic enzyme β-glucosidase, also known as elaterase (isolated from the dried juice of *Ecballium elaterium* called elaterium). The first cucurbitacin, named elaterin, was isolated from elaterium in 1831. The α-elaterin (cucurbitacin E) is usually present as a monoglucoside but is easily hydrolyzed by the enzyme. On the contrary, other species such as *Citrullus colocynthis* lack this enzyme; therefore their cucurbitacins are not present as free genins (Benigni *et al.* 1962). Despite their toxicity, species in which they are found have been used for centuries in various pharmacopoeia. Nevertheless, these species are not widely used at present, and when they are, only under strict medical control. The general structure of the cucurbitacins is triterpenic signifying that they have 30 carbons. The C_4 carries a gem-dimethyl group and the C_{24} an isopropyl, other methyls are present on carbons C_9, C_{13}, C_{14}, and C_{20}. All of them have an unsaturated carbon C_5. The cucurbitacins are all named after successive letters of the alphabet from A to R (**Table 3**), although later another two, S and T, presenting a heterocycle were added. Also some iso forms are found in nature (*trans*-location of the C_2 and C_3 substituents), 23, 24 dihydro, 11 and 22-deoxo and 22 deoxo-iso. The most common in the plant kingdom are certainly cucurbitacins B and D, followed closely by E and later by G, H, and I.

Medicinal use

For its high content in aspartic acid, glutamic acid, alanine, proline, serine, tyrosine, threonine, and valine, chayote fruit is recommended in hospital diets (Flores 1989); there is evidence that the tea of *S. edule* leaves or fruits has diuretic effects and even destroys renal calculi; besides, it is complementary in the treatment of arteriosclerosis and hypertension (Bueno *et al.* 1970; Jensen and Lai 1986; Salama *et al.* 1986).

The attempts to explain some medicinal effects permitted to establish that chayote fruit extract reduces diastolic pressure, event accompanied by a reduction in glucose and globin levels (Diré *et al.* 2004). Besides the systemic effect, it has been proved that the aqueous extract of *S. edule* has antimutagenic potential in *Salmonella thiphimurium* strains, but not in lymphocytes (Yen *et al.* 2001), while the ethanol extracts of the fruit exert inhibiting activity on L-929 rat lung fibrosarcoma proliferation (unpublished), basic property of antineoplasic agents (Setzer and Setzer 2003). The fruit extract also reduces the radioactive mark of blood cells

Table 3 Structures of the most important cucurbitacins.

Cucurbitacin	Formula	C_1	C_2	C_3	C_5	C_9	C_{11}	C_{16}	C_{20}	C_{22}	C_{23}	C_{24}	C_{25}
A	$C_{32}H_{46}O_9$	—	—OH	=O	Δ	—CH_2OH	=O	—OH	—OH	=O	Δ	—	—$OCOCH_3$
B	$C_{32}H_{46}O_8$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—$OCOCH_3$
Dihydro-B	$C_{32}H_{48}O_8$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—$OCOCH_3$
Iso-B	$C_{32}H_{46}O_8$	—	=O	—OH	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—$OCOCH_3$
C	$C_{32}H_{48}O_8$	—	—	—OH	Δ	—CH_2OH	=O	—OH	—OH	=O	Δ	—	—$OCOCH_3$
D (elatericin A)	$C_{30}H_{44}O_7$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—OH
22-deoxo-D	$C_{30}H_{46}O_6$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	—	Δ	—	—OH
22-deoxo-iso-D	$C_{30}H_{46}O_6$	—	=O	—OH	Δ	—CH_3	=O	—OH	—OH	—	Δ	—	—OH
E (α-elaterin)	$C_{32}H_{44}O_8$	Δ	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—$OCOCH_3$
Dihydro-E	$C_{32}H_{46}O_8$	Δ	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—$OCOCH_3$
F	$C_{30}H_{46}O_7$	—	—OH	—OH	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—OH
Dihydro-FF	$C_{30}H_{48}O_7$	—	—OH	—OH	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—OH
G	$C_{30}H_{46}O_8$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—OH	—OH
H (24-epi-G)	$C_{30}H_{46}O_8$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—OH	—OH
I (elatericin B)	$C_{30}H_{42}O_7$	Δ	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—OH
Tetrahydro-I	$C_{30}H_{46}O_7$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—OH
11-deoxo-I	$C_{30}H_{44}O_6$	Δ	—OH	=O	Δ	—CH_3	—	—OH	—OH	=O	Δ	—	—OH
J	$C_{30}H_{44}O_8$	Δ	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—OH	—OH
K (24-epi-J)	$C_{30}H_{44}O_8$	Δ	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—OH	—OH
L (dihydro-I)	$C_{30}H_{44}O_7$	Δ	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—OH
O (3-epi-F)	$C_{30}H_{46}O_7$	—	—OH	—OH	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—OH
P	$C_{30}H_{48}O_7$	—	—OH	—OH	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—OH
Q (acetyl-O)	$C_{32}H_{48}O_8$	—	—OH	—OH	Δ	—CH_3	=O	—OH	—OH	=O	Δ	—	—$OCOCH_3$
R (dihydro-D)	$C_{30}H_{46}O_7$	—	—OH	=O	Δ	—CH_3	=O	—OH	—OH	=O	—	—	—OH

(Diré *et al*. 2003), even some components seem to interact directly with DNA since they induce its breaking, possibly because of the induction towards new oxygen-reactive species (Diré *et al*. 2004). So far, the molecule (or molecules) responsible for modulating antimutagenic activity and inhibiting cell proliferation or DNA rupture have not been known. It has been demonstrated that antimutagenic activity of watery *S. edule* extract is present in small fractions with a molecular weight higher than 30 kDa, sensitive to heat, with 40% of phenolic content and high content of peroxidase activity (Yen *et al*. 2001).

Pharmacological effects

Species in which cucurbitacins are found, mainly those belonging to the Cucurbitaceae family (*Citrullus colocynthis* seeds, *Ecballium elaterium* fruits, *Bryonia* roots), have been used for centuries for their purgative properties. Their use, however, has diminished considerably due to their toxic nature since they manifest a hydragogue cathartic effect (Yesilada *et al*. 1988). However, some of them like *Momordica charantia* (African cucumber) and *M. blasamina* (Fatope *et al*. 1990) are still used to the present day.

On one hand, α-elaterin (cucurbitacin E) and elaterium, products with a well-known purgative effect, are not active in the absence of the spleen, thus suggesting an indirect action mechanism, secondary to a strong cholagogue or choleretic effect which has not yet been proved. On the other hand, cucurbitacin D increases intestinal movement *in vivo* but not in an isolated intestine (Edery *et al*. 1961). Cucurbitacins are well known to simulate secretions in the stomach due to their strong bitter flavor which has motivated the use of some species that contain them, e.g. *M. charantia* and *M. balsamina* (Fatope *et al*. 1990) as stomachics (eupeptic).

Cucurbitacin species have been used in folk medicine for the treatment of liver ailments for a long time. *Anagallis arvensis* is used as a hepatic therapy in Taiwan (Yamada *et al*. 1978). The species *Cucumis melo* containing cucurbitacins B and E is a remedy in Chinese traditional medicine (Tian Gua Di) for hepatitis (Hu *et al*. 1982). Cucurbitacin B has been shown to be effective in chronic hepatitis by normalizing hepatic protein levels, stimulating cellular immunity functions and increasing the *AMPc/GMPc* ratio in the plasma of experimental animals. These effects are all beneficial in the prevention or cure of hepatitis. In fact cucurbitacin B (0.2 mg kg^{-1}, i.v.) decreases levels of GPT, hepatic collagen and β-lipoproteins in rats with experimental fatty liver (CCI_4-induced) thus decreasing hepatic damage (cirrhosis, fibrosis). Cucurbitacin E (0.2 mg kg^{-1}, i.v.) also increases the *AMPc/GMPc* ratio from 1.95 to 2.56 which indicates a possible cucurbitacin action mechanism in the liver (Anonymous 1982).

Antineoplasic activities

Cucurbitacins have strong cytotoxic and antitumor action. This has motivated numerous tests in an attempt to prove, sometimes successfully, their possible anticarcinogenic activity. We are therefore faced with substances of unknown potential, many of which are antileukemic in experimental animals. Cucurbitacin B, iso-cucurbitacin B and the plant species in which they are found have been shown to be strongly cytotoxic (ED_{50} 10^{-5} µg mL^{-1} and 7.6 x 10^{-5} µg mL^{-1}, respectively) when tested on KB cell cultures proceeding from human nasopharyngeal carcinomas (Bean *et al*. 1985). Doskotch *et al*. (1969) in assays on the same cells concluded that cucurbitacin B was the principal substance responsible for the cytotoxic action of *Begonia tuberhybrida* var. *alba*. Previously, cytotoxic activities of cucurbitacins B, E, O, P, and Q had been demonstrated in similar cell cultures (KB). Their efficacy was lower *in vivo* (Kupchan *et al*. 1967) shown by a narrow therapeutic margin against Walker's intramuscular carcinoma in rats and Lewis's pulmonary carcinoma in mice (Lavie and Glotter 1971). Cucurbitacins B, D, E, I, J, K, L, (also found in *S. edule*) and tetrahydro-I isolated from *Bryonia alba* roots, all revealed cytotoxic activity in HeLa and KB human cell cultures (ED_{50} = 0.005- 1 µg mL^{-1}) with the first four substances being the most effective (Konopa *et al*. 1974a, 1974b). Cucurbitacin B shows strong cytotoxic activity against KB cells and HeLa and potent antitumor activity against 280 sarcoma and Ehrlich ascites carcinoma in mice (Gallily *et al*. 1962; Konopa *et al*. 1974b). Studies carried out by GISeM show that ethereal extracts of *S. edule* fruits var. *amargus silvestrys*, *nigrum spinosum*, *n. xalapensis*, *albus dulcis*, and *a. levis* have cytotoxic activity in the proliferation of leukemia fibroblast (P-388) and lung fibrosarcoma (L-929) though the extract of *n. levis* promotes it at low doses in both lines. In cervico-uterine cancer (HeLa) the methanol extract of *n. spinosum* showed outstanding cytotoxic activity at low doses.

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Throughout this review it has been proved that *S. edule* is an important phytogenetic resource for food and agriculture, mainly due to the wide range of biologic types within an infraspecific complex, which, we hope, will continue to increase its variation through the co-existence with the human groups, that have made it part of their culture. However, it has been just one of its varieties, which has received major attention, on the markets as well as by researchers (var. *virens levis*), while for the rest of the varieties, there do not exist so many studies. It is important to consider that to depend on only one variety in commercial terms causes different associated risks, which may include from unpredictable changes in consumption tendencies in the medium and the long term, phytosanitary fragility, due to genetic uniformity in the crop areas, until provoking involuntarily genetic erosion of chayote varieties of less commercial preference with potential impact on the loss of the genetic reserve of the species.

The aforesaid is not exclusive for the producer regions of Mexico, since this also happens in Costa Rica, which is the main chayote exporter world-wide. This suggests continuing to develop research programs which may recover and incorporate most of the chayote varieties, with the final purpose to increase the knowledge that permits its conservation. Regarding this, in Mexico GISeM has implemented a National Program of Conservation and Research of biodiversity of chayote (*Sechium edule* (Jacq.) Sw.), whose objectives involve its position as a species of national priority, collecting, describing from morphological aspects to molecular characteristics and conserving its biodiversity, searching for potential pharmacological uses, developing basic and technological research. All this knowledge generated is linked with technological transfer. Furthermore, techniques are being developed, such as the improvement and development of new presentations of the fresh product with the purpose of providing the consumer with high quality, healthy and innocuous fruits of chayote.

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