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Consensus Document on the Biology of Tomato

(*Solanum lycopersicum* L.)

Environment Directorate

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FOREWORD

Consensus Documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, these are being published on information on the biology of certain plant species, selected traits that may be introduced into plant species, and biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of Tomato *(Solanum lycopersicum* L.*)*.

Spain and Mexico served as the co-leads in the preparation of this document, and the draft has been revised based on the input from other member countries and stakeholders.

This document is published under the responsibility of the Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology.

TABLE OF CONTENTS

Tables

INTRODUCTION

1. The cultivated tomato, *Solanum lycopersicum* L., is the world's most highly consumed vegetable due to its status as a basic ingredient in a large variety of raw, cooked or processed foods. It belongs to the family Solanaceae, which includes several other commercially important species. Tomato is grown worldwide for local use or as an export crop. In 2013 the global area cultivated with tomato was 4.7 million hectares with a production of 163 million tonnes, the major tomato producing countries being China and India (FAOSTAT, 2015). Tomato can be grown in a variety of geographical zones in open fields or greenhouses, and the fruit can be harvested by manual or mechanical means. Under certain conditions (e.g., rejuvenation pruning, weeding, irrigation, frost protection), this crop plant can be perennial or semi-perennial, but commercially it is considered an annual (Geisenberg and Stewart, 1986).

2. Although there are many types of growing systems for greenhouse tomatoes, the two principal cropping systems are: two crops per year; and one crop per year. Its importance lies not only in profit, but also in the income generated in local economies for farmers and agricultural workers (Villarreal, 1982; Coll-Hurtado and Godínez Calderón, 2003). Protected agriculture is a wide category of production methods providing some degree of control over various environmental factors. This category includes production technologies such as: greenhouses, glasshouses, tunnels and covered fields (Nieves-García et al., 2011). Although there is no quantitative data about the world's vegetable production in greenhouses, some calculations have been made. For example, in 2012, the greenhouse vegetable production was about 81 million kilos, of which 40 million kilos was tomato, and 37 million kilos was cucumber. More specifically, in 2012, in North America the tomato production in greenhouses accounted for the 52% of the market in Canada and the 22% of the market in the US (Farm Credit Canada, 2012).

3. The commercially important tomato fruit can vary in colour, size and shape (Vaughan and Geissler, 1997). The fruit contains a large quantity of water, vitamins and minerals, low amounts of proteins and fats, some carbohydrates. It also contains carotenes, such as lycopene (which gives the fruit its predominantly red colour) and β-carotene (which gives the fruit its orange colour). Modern tomato cultivars produce fruits that contain up to 3% sugar of fresh fruit weight. It also contains tomatine, an alkaloid with fungicidal properties. The concentration of tomatine decreases as the fruit matures and tomatine concentration contributes to determining the taxonomy of the species. Thus it can be useful in crop breeding for cultivated tomatoes (OECD, 2008; Spooner et al., 1993).

4. Cultivated tomato is related to wild tomatoes originating from Peru, Ecuador and other parts of South America including the Galapagos Islands. The centre of its domestication and diversification is Mexico (Rick, 1978; Jenkins, 1948; Peralta et al., 2008). Wild relatives of tomato and intermediate forms (landraces or creoles) harbour a wealth of genetic diversity and are important sources of genetic material in crop improvement and conservation programmes (Sánchez-Peña et al., 2004).

5. Tomato is one of the best studied cultivated dicotyledonous plants at the molecular level and has been used as a model species for research into gene mapping, gene characterisation (e.g., plant pathogen resistance genes) and gene transfer approaches. It is also useful to study other plant traits such as fruit ripening, hormone function and vitamin biosynthesis (Gebhardt et al., 1991; Chetelat and Ji, 2006; Ji and Scott, 2006).

6. The common name known all over the world, tomato, originates from a Spanish usage assigned to the Mexican word in Náhuatl "xictomatl" ("xictli": navel and "tomatl": tomato), meaning the tomato with a navel. This refers to the scar left on the fruit by the peduncle. In Mexico the plant is frequently called "jitomate".

SECTION I - GENERAL DESCRIPTION AND TAXONOMY

1.1. General description

7. Tomato is a perennial herbaceous plant but it is often grown as an annual crop even if biennial and perennial forms exist. Tomato is cultivated in tropical and temperate climates in open field or under greenhouse in temperate climate. Greenhouses are often used for large scale production. In warm climate with the right light intensity for growth around 45 days are necessary from germination to anthesis and 90 to 100 days to reach to beginning of fruit ripeness (Nuez, 2001). The end use of the crop, whether for the processing market or fresh market will determine the cultivars sown, the time of harvest and harvest processes, which can be manual or mechanical (Nuez, 2001).

8. The growth habit of the plant varies from indeterminate to determinate and may reach up to 3 m in height. The primary root may grow several meters in length. The stem is angular and covered by hairy and glandular trichomes that confer a characteristic smell. Leaves are alternately arranged on the stem with a 137.5 degree phyllotaxy. Leaves range in shape from lobed to compound with segments arranged pinnately. Compound leaves are typically comprised of 5 to 9 leaflets. Leaflets are petiolated and dentated. All leaves are covered by glandular, hairy trichomes.

9. The tomato fruit is globular or ovoid. Botanically, the fruit exhibits all of the common characteristics of berries; a simple fleshy fruit that encloses its seed in the pulp. The outer skin is a thin and fleshy tissue that comprises the remainder of the fruit wall as well as the placenta. The colour of the fruit is derived from the cells within the fleshy tissue. Tomato fruits can be either bilocular or multilocular. Between 50 and 200 seeds are located inside the locular cavities and are enclosed in gelatinous membranes. On average, the seeds are small (5 x 4 x 2 mm) and lentil shaped. The seed contains the embryo and the endosperm and is covered by a strong seed coat, called the testa. The development of the fruit takes between 7 to 9 weeks after fertilization. The many end uses of tomato fruit, as well as food and feed safety considerations, including composition of key food and feed nutrients, anti-nutrients, allergens, and toxicants, are detailed in the OECD Consensus Document on Compositional Considerations for New Varieties of Tomato (OECD, 2008).

1.2. Taxonomy

10. The cultivated tomato is a member of the genus *Solanum* within the family *Solanaceae*. The *Solanaceae*, commonly known as the nightshade family, also includes other notable cultivated plants such as tobacco, chilli pepper, potato and eggplant.

11. Tomato classification has been the subject of much discussion and the diversity of the genus has led to reassessment of earlier taxonomic treatments. Tomato was originally named *Solanum lycopersicum* by Linnaeus in 1753; *Lycopersicon lycopersicum* (L.) Karsten has also been used (Valdes and Gray, 1998). Miller (1768) in The Gardener's Dictionary used *Lycopersicon esculentum*. Rick (1979) included nine species in the *Lycopersicon* genus. For a long time tomatoes were known as *Lycopersicon esculentum* but recent research has shown that they are part of the genus *Solanum* and are now again broadly referred to as *Solanum lycopersicum* (Spooner et al., 1993; Bohs and Olmstead, 1997; Olmstead and Palmer, 1997; Knapp, 2002; Spooner et al., 2005, 2003; Peralta, 2008).

12. The genus *Solanum* consists of approximately 1,500 species. The tomato clade (section *Lycopersicon*, formerly recognised as the genus *Lycopersicon*) includes the cultivated tomato (*Solanum lycopersicum*) and 12 wild relatives, all natives to western South America (see Table 1). Tomato (*Solanum lycopersicum*) is derived from two wild ancestor species *Solanum pimpinellifolium* and *Solanum cerasiforme*. Other wild species are useful for breeding disease resistance, colour improvement and desirable quality traits (Ranc et al., 2008). The twelve wild members of the *Lycopersicum* clade demonstrate a high level of phenotypic and genetic variation; including a great diversity in mating systems and reproductive biology (see Section IV and Bedinger et al., 2010). Peralto et al. (2006) recognised 12 species of wild tomato; this was an increase on the nine species of tomato recognised by Rick et al. (1990). Within these 12 species, informal species groupings were made: four closely related green-fruited species, *S. arcanum*, *S. huaylasense, S. peruvianum* and *S. corneliomulleri* were grouped in the *S. peruvianum sensu lato* (*sensu lato* refers to a broad concept of a species). Another group of yellow to orange fruited species contains two species endemic to the Galapagos Islands; *S. galapagense* and *S. cheesmaniae*.

13. Table 1 lists species belonging to the tomato clade, including the cultivated tomato (*S. lycopersicum*) and twelve wild tomato species, as well as four other closely affiliated *Solanum* species (Peralta et al., 2008). Table 2 lists tomato species for the genus *Solanum* subsect. *Lycopersicon* (USDA, 2009).

Table 1. **Taxonomy of the genus *Solanum* sect. *Lycopersicoides,* sect. Juglandifolia, sect. *Lycopersicon***

Species	Synonyms
S. lycopersicoides Dunal	*L. lycopersicoides* (Dunal) A. Child ex J.M.H. Shaw
S. sitiens I.M.Johnst	*L. sitiens* (I.M.Johnst) J.M.H. Shaw
S. juglandifolium Dunal	*L. juglandifolium* (Dunal) J.M.H. Shaw
S. ocharanthum Dunal	*L. ocharanthum* (Dunal) J.M.H. Shaw
S. pennellii Correl	*L. pennellii* (Correl) D´Arcy
S. habrochaites S.Knapp & D.M.Spooner	*L. hirsutum* Dunal
S. chilense (Dunal) Reiche	*L. chilense* Dunal
S. huaylasense Peralta	partly *L. peruvianum* (L.) Miller
S. peruvianum L.	*L. peruvianum* (L.) Miller
S. corneliomulleri J.F.Macbr.	partly *L. peruvianum* (L.) Miller
(1 geographic race Misti near Arequipa)	also known as *L. glandulosum* C.F.Müll
S. arcanum Peralta	partly *L. peruvianum* (L.) Miller
(4 geographic races humifusum, lomas, Marañon, Chotano-Yamaluc)	
S. chmielewskii (C.M.Rich et al.)	*L. chmielewskii* C.M.Rich et al. D.M.Spooner et al.
S. neorickii D.M.Spooner et al.	*L. parviflorum* C.M.Rich et al.
S. pimpinellifolium L.	*L. pimpinellifolium* (L.) Miller
S. lycopersicon L.	*L. esculentum* Miller
S. cheesmaniae (L. Riley) Fosberg	*L. cheesmaniae* L. Riley
S. galapagense S.C. Darwin & Peralta	Partly *L. chesmaniae* L. Riley

Source: Peralta et al., 2008

Table 2. **Taxonomy of the genus *Solanum* sect. *Lycopersicoides***

1. ***Solanum agrimoniifolium*** (Dunal) J. F. Macbr. (subgroup. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   = *Solanum habrochaites* S. Knapp & D. M. Spooner
2. *Solanum arcanum* Peralta (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms: (=) *Lycopersicon peruvianum* var. *humifusum* C. H. Müll.
3. *Solanum caldasii* Dunal (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Juglandifolia*)
   = *Solanum ochranthum* Dunal
4. *Solanum cheesmaniae* (L. Riley) Fosberg (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms: (≡) *Lycopersicon cheesmaniae* L. Riley
5. *Solanum chilense* (Dunal) Reiche (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms: (≡) *Lycopersicon chilense* Dunal
6. *Solanum chmielewskii* (C. M. Rick et al.) D. M. Spooner et al. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms:
   (≡) *Lycopersicon chmielewskii* C. M. Rick et al.
7. *Solanum corneliomulleri* J. F. Macbr. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms**:**
   (≡) *Lycopersicon glandulosum* C. H. Müll.
8. *Solanum galapagense* S. C. Darwin & Peralta (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms:
   (=) *Lycopersicon cheesmaniae* var. *minor* (Hook. f.) D. M. Porter
   (=) *Lycopersicon cheesmaniae* f. *minor* (Hook. f.) C. H. Müll.
9. *Solanum habrochaites* S. Knapp & D. M. Spooner (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
   Synonyms**:**
   (=) *Lycopersicon agrimoniifolium* Dunal
   (≡) *Lycopersicon hirsutum* Dunal
   (=) *Lycopersicon hirsutum* f. *glabratum* C. H. Müll.
   (=) *Solanum agrimoniifolium* (Dunal) J. F. Macbr.
10. *Solanum huaylasense* Peralta (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
11. *Solanum juglandifolium* Dunal (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Juglandifolia*)
12. *Solanum lycopersicoides* Dunal (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Lycopersicoides*)
13. *Solanum lycopersicum* L. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
14. *Solanum lycopersicum* var. *cerasiforme* (Alef.) Fosberg (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms:
    (≡) *Lycopersicon esculentum* var. *cerasiforme* Alef.
    (≡) *Lycopersicon lycopersicum var. cerasiforme* (Alef.) M. R. Almeida
15. *Solanum lycopersicum* var. *lycopersicum* (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms:
    (≡) *Lycopersicon esculentum* Mill.
    (=) *Lycopersicon esculentum* var. *commune* L. H. Bailey
    (≡) *Lycopersicon esculentum* var. *esculentum*
    (=) *Lycopersicon esculentum* var. *grandifolium* L. H. Bailey
    (=) Lycopersicon esculentum f. *pyriforme* (Dunal) C. H. Müll.
    (=) *Lycopersicon esculentum* var. *pyriforme* (Dunal) Alef.
    (=) *Lycopersicon esculentum* var. *validum* L. H. Bailey
    - (≡) *Lycopersicon lycopersicum* (L.) H. Karst.
    - (=) *Lycopersicon lycopersicum* var. *pyriforme* auct.
    - (=) *Lycopersicon pyriforme* Dunal

Table 2. **Taxonomy of the genus *Solanum* sect. *Lycopersicoides* (Continued)**

16. *Solanum neorickii* D. M. Spooner et al. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms**:**
    (=) *Lycopersicon parviflorum* C. M. Rick et al.
17. *Solanum ochranthum* Dunal (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Juglandifolia*)
    Synonyms**:**
    (=) *Solanum caldasii* Dunal
18. *Solanum pennellii* Correll (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms**:**
    (≡) *Lycopersicon pennellii* (Correll) D'Arcy
    (≡) *Lycopersicon pennellii* var. *pennellii*
    (≡) Lycopersicon pennellii var. *puberulum* (Correll) D'Arcy
    (=) *Solanum pennellii* var. *elachistus* Martic. & Quezada
    (=) *Solanum pennellii* var. *pennellii*
    (=) *Solanum pennellii* var. *puberulum* Correll
19. *Solanum pennellii* var. *elachistus* Martic. & Quezada (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    = *Solanum pennellii* Correll
20. *Solanum pennellii* var. *pennellii* (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    = *Solanum pennellii* Correll
21. *Solanum pennellii* var. *puberulum* Correll (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    = *Solanum pennellii* Correll
22. *Solanum peruvianum* L. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms**:**
    (=) *Lycopersicon dentatum* Dunal
    (≡) *Lycopersicon peruvianum* (L.) Mill.
    (=) *Lycopersicon peruvianum* var. *dentatum* (Dunal) Dunal
    (≡) *Lycopersicon peruvianum* var. *peruvianum*
23. *Solanum pimpinellifolium* L. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*) Synonyms**:**
    (≡) *Lycopersicon esculentum* subsp. *pimpinellifolium* (L.) Brezhnev
    (≡) *Lycopersicon esculentum* var. *racemigerum* (Lange) Brezhnev
    (≡) *Lycopersicon pimpinellifolium* (L.) Mill.
    (=) *Lycopersicon racemigerum* Lange
24. *Solanum rickii* Correll (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Lycopersicoides*)
    = *Solanum sitiens* I. M. Johnst.
25. *Solanum* sect. *lycopersicon* hybr. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms**:**
    (=) *Lycopersicon* hybr.
    Solanum sect. *lycopersicon* spp. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Neolycopersicon*)
    Synonyms:
    (=) *Lycopersicon* spp.
26. *Solanum sitiens* I. M. Johnst. (subg. *Potatoe* sect. *Petota* subsect. *Lycopersicon* ser. *Lycopersicoides*
    Synonyms**:**
    (=) *Solanum rickii* Correll

Source: United States Department of Agriculture, Agricultural Research Service (2015)

1.3 Geographic Distribution, Centre of origin and domestication, Cultivation and Management Practices

14. In the case of cultivated plants, in addition to the centre of biological origin, other areas exist where wild ancestors and other related forms in an incipient stage of domestication (e.g., weed forms and local landraces) coexist. This area, known as the centre of genetic diversity, contains an extraordinary diversity of forms. Harlan (1973) defined geographic areas different from the natural centre of distribution of the crop as secondary centres or centres of trans-domestication. These are the zones where the species is domesticated. Occasionally, both areas coincide. In the case of tomato, its centre of origin and its centre of diversity are different (Harlan, 1971).

1.3.1. Natural Centre of Origin

15. The natural geographic distribution or centre of origin of *Solanum lycopersicum,* (*S.* section *Lycopersicon*) has been localised in the narrow band between the Andes mountain ranges and the Pacific coast of western South America (WWF and IUCN, 1997). This extends from southern Ecuador to northern Chile, including the Galapagos Islands (Peralta et al., 2008; Nuez et al., 1996; Jenkins, 1948). This is based on the geographic distribution of the native wild ancestors of the genus between coordinates 0º-20º S and 64º-81º W where they grow spontaneously and sympatrically (Taylor, 1986).

16. Based on research from the Tomato Genome Consortium 2012, the three wild species most closely related to cultivated tomato include the red-fruited species *S. pimpinellifolium* and the orange-fruited species found on the Galapagos Islands, *S. galapagense* and *S. cheesmaniae* (Menda and Mueller, 2013).

17. Mexico is presumed to be the most probable region of domestication, with Peru as the centre of diversity for wild relatives (Larry and Joanne, 2007). *Solanum lycopersicum cerasiforme* is thought to be the ancestor of cultivated tomato, based on its wide presence in Central America and the presence of a shorten style length in the flower (Cox, 2000).

1.3.2 Centre of Domestication

18. During prehispanic times, various useful plants were introduced and domesticated in Mesoamerica from South America. The original South American tomato fruit became a synanthrophyte, a plant species brought indirectly to Mexico through trade between prehispanic cultures. The characteristics of this wild fruit were different from the cultivated fruit: small size (1-2 cm diameter), bilocular, and acid taste (Jenkins, 1948). Upon its arrival in Mesoamerica, its similar morphology with the green tomato (*Physalis*) facilitated its adoption and adaptation by Mexican cultures. Since those times, the use and diversification in morphotypes, dimensions, forms and colours of the fruits used as food by Mexican indigenous cultures were extraordinary (Sahagún, 1979). As such, Mexico, together with the Andes zone, houses the largest morphological variability in tomato (Rick, 1978; Jenkins, 1948) and is considered the centre of diversity and domestication of S. *lycopersicum* (Larry and Joanne, 2007; Nuez, 1996; Rick, 1990; Jenkins, 1948).

1.3.3 Crop migration

19. Historical records allow the reconstruction of the arrival of tomatoes in the Old World, following European contact. The Spanish navigators brought seeds to Europe in the 16^{th} century and friars sent some of these to their brothers. The tomato first arrived in Andalusia (via the Canary Islands) and was dispersed throughout Spain. The Spanish and the Italians were the first to accept this "exotic" fruit. According to Mattioli (Nuez et al., 1996; Rick, 1978), it was consumed with oil, salt and pepper in Italy. In other European countries, acceptance was slow and the tomato long remained an ornamental plant because of the

fear of poisoning or "the curse of the dulcamara" (Long Towell, 2001). This belief was associated with the toxic, hallucinogenic and aphrodisiac properties of other members of the Solanaceae, such as Belladona (*Belladona*) and Mandragora (*Mandragora*), which have detrimental effects on health caused by some alkaloids (OECD, 2008).

20. The first mention of tomato in England was by the botanist Gerard in 1597. Besler (1613), a German naturalist, first showed engravings of tomato plants present at the Eichstätt Garden in Germany. Considering the size of the fruit shown in the engravings, it is assumed that they depict plants already domesticated as ornamentals. In 1760, tomato was represented as an ornamental in the Andrieux-Vilmorin catalogue in France (Fournier, 1948).

21. Tomato returned to the Americas in the 18th century, according to reports of its cultivation in the West Indies and the Caribbean. Tomato was also transported to North America in the 18th century by European colonists arriving at commercial harbours in New Jersey, the United States. The first written account dates from 1710, when it was registered as an ornamental plant by William Salmon. However, it was not trusted as a foodstuff in the United States until the beginning of the 20th century because of its similarity to certain poisonous fruits (Rick, 1978).

22. Knowledge of the tomato's nutritional importance increased from the end of the 19th century to the beginning of the 20th century (Rick, 1978). The first improved tomatoes were developed by Italian breeders in the 17th or early 18th century, who converted the small, wrinkled and hard tomato into the red coloured, smooth and juicy varieties known today (Atherton and Rudich, 1986; Rick, 1976). Starting from these cultivars, the United States began in 1867 the production of various cultivars and nine commercial varieties (Early Smooth, The Cook's Favorite, Tildem, Powells Early, FEUE, Large Red, Large Yellow, Tree Tomato red and Yellow Plum) (Atherton and Rudich, 1986).

23. Tomato is now a cosmopolitan crop with major production in temperate regions, even though its origins lay in tropical regions.

1.3.4 Evolution of cultivation

24. Tomato has been cultivated since Prehispanic times with the earliest agricultural techniques, and its cultivation and production keep improving and evolving. This depends on several factors such as the organoleptic properties of the fruits, farming system, soil type, environmental conditions, the crop variety used, degree of technological development and capital available, as well as the goal of the production.

25. The first methods of cultivation developed within the Mesoamerican farming system of milpa, a polyculture association of maize (*Zea mays*), beans (*Phaseolus* spp.) and squash (*Cucurbita* spp.). This trilogy is an important source of carbohydrates, proteins and fats. Moreover, other species found in milpa, such as chili pepper and tomato, provide vitamins and minerals, so that this production system satisfies nearly all nutritional necessities. The milpa was the first home of tomato; it arrived in Mexico as a synanthrophyte and incorporated itself in the local production systems. It underwent the same selection processes as other useful weeds: collected, tolerated [a weedy variant of tomato called "tomate de culebra" (snake tomato) is still tolerated], and/or protected within cultivation (Casas, 2001). Subsequently, by attracting human attention as an edible plant, it was subject to a more intensive selection process in combination with a habitat change. Cultivation and management practices provided it with better environmental conditions which induced better production (Zizumbo, 1986).

26. Traditional farming systems are also a reservoir of available genetic resources. Cultivating plants, while allowing their coexistence with their wild or weedy relatives, can conserve crop genetic resources.

1.3.5 Crop production

27. About 163 million tonnes of tomatoes are harvested annually from plantings of 4.7 million hectares. About 60% of world production comes from Asia, 11.1% from Africa, 12.8% from Europe, 7.9% from North America and 6.5% from Central America and South America (FAOSTAT, 2015). According to FAOSTAT 2015, the top five world's greatest producers of tomato in 2013 were China, India, the USA, Turkey and Egypt. Tomato is considered to be one of the most important vegetables produced in commercial agriculture because it is cultivated in temperate and warm regions of the world and it generates cash as an export crop.

1.3.5.1. Climate

28. Tomatoes require a warm climate for growth and do not tolerate frost. The usual life cycle in cultivation spans one spring and summer. Its optimum temperature is around 26 ºC (day) and 12 ºC (night). Plants require minimum temperatures above 18 ºC for vegetative growth, but can survive at lower temperatures (12 ºC). Temperatures above 31 ºC reduce the rates of flower fertilisation, plant development and fruit ripening. Table 3, adopted from Geisenberg and Stewart (1986), lists the optimal temperature ranges required at different stages of tomato development.

Table 3. **Temperature ranges**

Stages of plant development	Temperature °C		
	Minimum	Optimum	Maximum
Germination	11	15-30	30
Vegetative growth	18	20-24	30
Fruit -set night	10	14-20	24
Fruit -set day	18	20-24	30
Red colour development	10	20-24	30

Source: Garza and Molina, 2008; Nieves-García et al., 2011.

29. Air relative humidity between 55-60% is important for effective pollen production and pollination.

1.3.5.2 Soil

30. Tomatoes grow well on most mineral soils, but they prefer deep, well drained sandy loams. Deep tillage enables adequate root penetration in heavy-clay-type soils thus allowing the production of tomato in them. Tomato is a crop moderately tolerant to a wide range of pH. Worley (1976) showed that tomato yield was higher in soils with a pH between 6.5 and 6.9 compared with that obtained in acidic soils. Soils with acidic pH or salinity lead to a decrease in the size of the fruit (Doss et al., 1977; Papadopoulos and Rendig, 1983).

1.3.5.2.1 Soil preparation

31. This practice plays a role in the establishment of the crop, either by direct seed sowing or transplantation.

1.3.5.3 Nutrient requirements

32. Nutrient requirements of the tomato crop depend on variety, yield and cultural practices (for instance, see Sainju et al., 2003). Soil and tissue analyses should be taken throughout the growing and production season to ensure essential nutrients are present in their proper amounts and ratios. We can consider the following nutrient requirements as average: 30 t/ha organic matter; 50 kg/ha N; 80-100 kg/ha P; 200-250 kg/ha K. Under greenhouse conditions the nutrient doses can be higher to increase the yield. Fertiliser use is limited in organic production and it may also be limited in conventional production in some countries due to the cost.

1.3.5.4 Seedling nursery

33. This practice is aimed to obtain vigorous, healthy and uniformly growing seedlings, optimal for transplantation and assuring 100% survival in the field or greenhouse. Overseeding (relative to the number of transplants needed) is required to compensate for a lack of germination or emergence and seedling death. It is also important to have additional transplants in order to select a vigorous, uniform group for transplanting. The percent of seedlings lost for reasons listed above vary by operation and situation. In general, lack of germination (10 %) or emergence (10 %) and seedling death (5 %) may require overseeding by up to twenty-five percent.

1.3.5.5 Transplantation

34. The field which will receive the seedlings must be humid and holes must be made in order to deposit the seedlings. These must be removed from the seedbed avoiding physiological damage to the roots. The periods of transplantation are generally from May to June in the Northern hemisphere. However, there are cultivated varieties which are planted from November till February. Planting distance is 25 to 50 cm between seedlings and 1.50 to 1.80 m between rows.

35. Planting distance changes with production goal: for fresh consumption, 22,000 to 25,000 plants/ha; and for industry, 40,000 to 60,000 plants/ha.

1.3.5.6 Fertilisation

36. In general, fertiliser is applied during three stages: first, before transplantation; second, 60 days afterwards; and third, after 100 days. Fertilisation is limited in organic production; and in some countries (e.g., the Netherlands) also in conventional production.

1.3.5.7 Irrigation

37. Tomato requires frequent irrigation to delay maturity and prolong plant productivity. Irrigation also helps to reduce salinisation. Some authors suggest that soil moisture levels should never exceed 0.2 bars, whereas other authors suggest a maximum of 2 bars (see irrigation chapter in Nuez, 2001). The recommended soil moisture level varies with cultivation method, variety and climate (Castilla, 1995). Erratic moisture conditions can cause radial and concentric cracking on the fruit (Peet and Willits, 1995). This is a serious physiological disorder that leaves the affected tomatoes unmarketable and leads to quick deterioration. Moisture requirements vary with crop variety, prevailing climate and soil characteristics.

38. Tomatoes in fields or glasshouses can be grown in polyethylene-mulched beds with drip irrigation which allows for close monitoring of nutrients. The plastic mulch helps to maintain a high efficiency in the use of water and fertiliser (Jensen et al., 1989). Drip irrigation for tomatoes has gained popularity as it increases water use efficiency and also allows the application of fertilisers mixed in the irrigation water. With drip irrigation it is possible to closely synchronise weekly water and nutrient application rates with the corresponding stage of crop development.

1.3.5.8 Pruning and guidance of the plants

39. Through pruning, shoots appearing in leaf axils are removed to create a plant architecture which facilitates management. The advantages of pruning are: stimulation of plant development, more efficient phytosanitary control and achievement of higher quantitative and qualitative yield. Pruning of leaves is necessary for phytosanitary control, and a vegetative balance and generative control. Plants may be supported by a trellis e.g. 2 m posts (sunk to 50 cm) positioned at regular intervals of 3-5 m support cotton threads or galvanised metal wire to lift and support the plant and facilitate access for crop management and pest control.

1.3.5.9 Earthing-up

40. Earthing-up consists of massing up earth at the plant base with the aim to assure the growth of adventitious roots providing better anchorage. The first earthing-up occurs between the 1st and 2nd week after transplantation and is repeated between the 4th and 5th week. On occasion, this practice is also performed during weeding.

1.3.5.10 Harvest

41. The level of maturity at which fruits are harvested depends on the final production goal. The harvest interval may continue up to 7 months.

Table 4. **Harvest indicator**

Production goal	Harvest indicator
Local consumption	Turgid fruits with intense red colour
Regional consumption	Pink fruits
Export	"Green-mature". Because of semi- and long life varieties, it is now common in Europe to export tomato with red colour making use of colour tables or instruments
Industry	Physiologic maturity; there is no explicit colour

Source: Garza and Molina, 2008; Nieves-García et al., 2011.

42. Farming practices described above may be adapted for the open field, as well as for protected cultivation and intensive farming systems. Agricultural techniques for the cultivation of tomato are an integral part of culture and should be applied according to the type of crop that will be sown. As such, they will be listed below in a general manner. Beside this, one of the most important factors affecting yield and quality obtained in tomato production is the occurrence and effects of pests and diseases. Major tomato pests and diseases are listed in Appendices 1 and 2 respectively.

1.3.6. Production in Modern and Intensive Systems

43. With the help of advances in modern technology, tomato can now be cultivated in both tropical and temperate zones in the open field, in home gardens, in small-scale agricultural patches or as large-scale urban market production or agro-industry. It can be found in traditional farming systems (shifting cultivation) as well as in modern and intensive systems using acclimatised greenhouses, plastic cover nurseries, hydroponics and fertigation. This vegetable species is adapted to grow under different environmental and cultural conditions (OECD, 2008).

44. Due to climatic variations, like low temperatures in North America and Europe during a large period of the year, as well as cloudiness and high precipitation in tropical and subtropical regions of the world, it has been necessary to search for alternative protected production systems. Greenhouse production is an alternative intensive production system. Its objective is to obtain higher production levels per area unit by controlling nutrition, temperature and light among other conditions that affect plant growth.

45. Adding up to the structural characteristics and energy input of the greenhouse, the crop’s morphological characteristics as well as its physiological requirements and cultivation practices must be considered (Berenguer, 2003; Castilla, 2003). As such, sowing density, pruning techniques, fertiliser concentrations, etc., will depend largely on the sown crop variety.

46. This concept is sustained within new proposals of tomato production systems. As an alternative of the general protected cultivation concept through improvement of plants environmental conditions in order to augment yield, there exist the Mediterranean greenhouses, based on a minimal or almost zero energy input inducing minimal modifications in the microclimate (Enoch, 1986; Monteiro, 1990).

47. A result of the use of micro environmental modifications is the use of the so-called “biospaces”, the combined effort of efficient agronomic practices and micro environmental modification (mesh, cloth and pipes) in zones with high radiation and temperature and low relative humidity in order to favour growth and development of fruity vegetables (Bustamante, 2003).

48. A cultivation technique which can be combined with the biospace is the plastic cover nursery. This involves complete ground cover around the crop with plastic in order to detain weed growth, diminish humidity loss and improve fertility. These advantages are the result of the temperature increase under the plastic and in combination with the retained humidity, this stimulates processes of nitrification and solubility of salts causing germinating weeds to be killed.

49. Nowadays, the intensive greenhouse production of tomato involves the use of hydroponics, a production system in which the roots are irrigated with water containing a mix of essential nutritional elements while sustained in a substrate of inert material or the same solution instead of soil (Sánchez and Escalante, 1981).

50. Vegetable grafting is gaining interest in open-field and high tunnel tomato production. There are a variety of grafting techniques, but the most widely adopted method worldwide for grafted tomato production is tube grafting. Resistant rootstocks are available for tomato, and can be used to manage

economically important soil borne pathogens such as *Ralstonia solanacearum* and root-knot nematodes (*Meloidogyne* spp.) or *Sclerotium rolfsii* (Rivard et al., 2010).

51. A new production alternative is ecological agriculture or the production of healthy and innocuous products while conserving basic natural resources like water, soil and biodiversity (García and Hernández, 2004).

52. An organic production system of tomatoes does not use chemical products, applies integrated pest management, occupies ten times less area and achieves prices ten times higher than conventional cultivation (Navejas et al., 2002).

SECTION II - REPRODUCTIVE BIOLOGY

2.1 Floral biology

53. Although some tomato wild species of the genus *Solanum* are allogamous, all commercial tomato cultivars are considered to be mainly self-compatible and inbreeding, *i.e.* autogamous (Rick, 1979; Taylor, 1986). Tomato flowers are perfect, regular and hypogynous and are borne on inflorescences that may be either determinate (cymose) or indeterminate (racemose), depending on the species. The flower is connected to the axis by a pedicel that includes the abscission point. The first flower appears when the plant has three leaves and, frequently, the first and the last bud of an inflorescence are aborted. The timing of floral landmarks for *S. pimpinellifolium* is described in detail in Buzgo et al., (2004). The number of flowers produced by an inflorescence is dependent upon environmental factors. A plant growing at 16 ºC produces four times more flowers than a plant growing at 24 ºC. Temperatures below 10 ºC, or less than 12 hours of light, reduce yield by causing premature flower abscission. As flowers form sequentially, buds, flowers and fruits can coexist in an inflorescence (Chamarro, 1995). The flowers are yellow and generally less than 2.5 cm in diameter when in full bloom. They possess four helically arranged whorls of organs; green sepals form the outer whorl or calyx, at least five yellow petals are present in the corolla, stamens alternate with petal position and are fused to form an anther cone and a whorl of two or more fused carpels form the pistil at the centre of the flower. The number of carpels found in the pistil varies between species and relates to the number of locules present in the resulting fruit.

2.2. Pollination, pollen dispersal, pollen viability

54. For some varieties, flowers have the style shorter than the tip of the anther cone, while for other varieties the style is longer than the anther cone. The stigma is receptive from 1-2 days before to 4-8 days after its own flower releases pollen, thus cross-pollination is possible. The first meiosis during pollen production occurs when the anthers reach one third of their final length. The optimal temperature range for pollen production is 10 to 35 ºC and the number of pollen grains formed in an anther is genetically determined. Anther dehiscence delivers thousands of pollen grains into the channel formed by the hairs. However, as anthers release pollen inwardly towards the style, vibration-assisted self-pollination is usual, especially in short-style varieties. In long-style varieties, the downward posture of the flower allows self-pollination by gravity. The anther cone releases pollen around the stigma at the slightest vibration. Wind and insects provide the vibrating action necessary for self-pollination under field conditions. Under greenhouse conditions mechanical vibrating devices or insects are used. Optimal conditions for pollination are temperatures of 17-24 °C and humidity above 70%. High humidity and low temperatures favour outcrossing (Nuez, 2001).

55. As is the case for most self-pollinating plants, the viability of exposed tomato pollen is limited. Pollen viability and the number of pollen grains are reduced by high temperatures above 32/26 °C day/night. The effect of temperature is associated with alterations in carbohydrate metabolism during another development (Pressman et al., 2002; Firon et al., 2006). Natural cross-pollination rates among commercial varieties range from 0.07% to 12% (Richardson and Alvarez, 1957; Groenewegen and George, 1994; Accotto et al., 2005). The rate of crossing quickly decreases as the distance from the pollen source increases (Currence and Jenkins, 1942) and little viable pollen is transferred beyond 30 m (~95 feet) from its source (Quiros and Marcias, 1978). The distance required between foundation seed fields in United

States is 200 feet (~61 m) which, in practical terms, is considered the security isolation distance that assures that a pollen grain cannot pollinate under field conditions (Rick et al., 1976).

56. Although tomato is generally self-fertile, cross-pollination between species is possible (discussed further in Section V “Genetics and Crosses”) and fruit set is similar in self- or cross-pollinated plants (Free, 1993). Male-sterility exists in tomato and, as this condition precludes self-fertilisation, such plants can be used to produce hybrid seed. Cross-pollination of male-sterile flowers is achieved by insect activity, rather than by wind or mechanical vibrators as employed for self-fertilisation (McGregor, 1976). Despite an extensive history of use (Section 1), a search of the relevant literature yields a surprising lack of data relating to basic biological characteristics of the domesticated tomato plant. In particular, it is difficult to find information that contributes to an understanding of the potential for gene flow (including pollen and seed dispersal) and data on seed viability or dormancy. These characteristics are generally understood to contribute to the potential weediness of a species. For tomato, the scarcity of information relating to such characteristics may be because it is not widely regarded as weedy (Randall, 2012). Keeler (1989) included tomato as a comparator (non-weedy) crop plant in a study on the potential for crop species to acquire weedy characteristics, noting a similar difficulty in acquiring information for non-weedy species.

2.3. Seed production and dormancy

57. The tomato seed matures from 35-50 days after pollination (DAP), during which seeds become germinable, desiccation tolerance is induced, and water content decreases. Fruit is red and ripe by 60 DAP. There are three stages of tomato seed development, the initial stage is morphogenesis, then maturation and finally seed quiescence.(DeCastro and Hilhorst, 2000). Primary dormancy occurs in tomatoes, where seeds become dormant during development, it is considered to assist plants to survive in periods of unfavourable growth conditions. Primary dormancy is often removed by exposure of dry seed to high temperatures or of imbibed seed to low temperatures and abscisic acid **(**ABA) is thought to play a part in breaking primary dormancy (Hillhorst and Downie 1995). However, tomato seed development appears to be independent of ABA (DeCastro and Hilhorst, 2000).

SECTION III - GENETICS

58. The new taxonomy adopted (Peralta et al., 2008) that include the former genus *Lycopersicon* under the genus *Solanum*, has also created and eliminated various species and modified certain sections of the genus. To be accurate with the work of the different authors in this section, the name used by them was maintained.

3.1 Genetics

59. Tomato is often used as a model system for diploid plant research into classical genetics, cytogenetics, molecular genetics and molecular biology. The advantages of using tomato for research have been reviewed by Ji and Scott (2006) and are summarised here as follows:

3.1.1 Genome size

60. Tomato has a relatively small genome size (around 950 Mb). About 30% of the genome is composed of repetitive sequences which are mainly located in heterochromatin regions (Van der Hoeven et al., 2002). Tomato and its wild relatives have 12 chromosomes (2n=2x=24). The 12 tomato chromosomes were first identified by Barton (1950).

3.1.2 Genetic mutation

61. Mutation has played an important role in tomato genetics. Spontaneous mutation is an important source of genetic variation (Chetelat and Ji, 2006). One spontaneous mutation, providing plants with determinate growth habit, has revolutionised tomato production (Atherton and Harris, 1986). Other mutations have been identified that confer male-sterility (Stevens and Rick, 1986) or cause aneuploidy (Ji and Chetelat, 2003). In addition, the use of artificial mutagenesis has led to the production of around 1 200 mutant lines that can be used for scientific research. Around 1 000 mutant loci have been characterised, 400 of which have been assigned to specific chromosomes (Chetelat, 2002; Chetelat and Ji, 2006). Monogenic mutants, markers, disease resistance genes and other types of stocks are maintained by the Tomato Genetic Resources Center (TGRC (http://tgrc.ucdavis.edu/)). The *Solanaceae* Genome network (SGN) maintains 13 000 M2 characterised families derived from tomato mutagenesis (http://zamir.sgn.cornell.edu/mutants/).

3.1.3 Chromosomal rearrangements

62. Variations have been produced at the chromosomal level with tomato euploids, haploids, triploids and tetraploids reported. Euploids have arisen spontaneously or have been produced by crosses between genotypes with different ploidy level. Haploids and triploids are meiotically instable and generally have low fertility, but tetraploids are meiotically stable and can be reproduced by seeds. Aneuploid variation of tomato at diploid level can occur by one of two ways: the deletion of a chromosome that produces monosomic lines that carry the monosome only in half of the gametes (Gill, 1983) and the addition of chromosomes that produces trisomics or alien addition lines. Complete sets of primary trisomics, and other types of trisomics derived from them, have been generated (Lesley, 1928; Khush and Rick, 1968). A complete set of tomato addition and substitution lines has been produced in the *S. lycopersicoides* background (Chetelat et al., 1998; Ji and Chetelat, 2003). Addition and substitution lines have also been

produced using *S. sitiens* (Pertuze et al., 2002). Chromosomal structural alterations have been identified in tomato (Gill, 1983; Khush and Rick, 1968). These chromosomal alterations have allowed the assignment of genes and markers (ex: QTLS) to specific chromosomes and have facilitated the establishment and orientation of genetic linkage maps.

63. Markers can be associated with chromosomes, parts of it, traits, genes etc. by studying its co-segregation with the chromosome, chromosomal fragment, trait or gene in question. When tightly linked to a gene or trait, markers can assist in breeding; particularly for traits as quantitative ones which need long and complex evaluation under field conditions.

3.1.4 Introgression lines

64. Introgression lines that contain chromosome segments from alien relatives in the background of the cultivated tomato greatly increase the genetic diversity available for improvement. They can also be advantageous for QTL (Quantitative Trait Locus) mapping and gene identification studies (Gur and Zamir, 2004) and have been used to develop numerous high-density molecular linkage maps, genomic data bases and DNA libraries. One series of 98 introgression lines has been obtained in which at least 85% of the genome of *S. habrochaites* f. *typicum* is represented in the background of *S. lycopersicum* (Monforte and Tanksley, 2000). The segments introgressed from *S. habrochaites* were identified by molecular markers and most of the lines were reasonably fertile. However, several lines were partially sterile, prompting a study of hybrid incompatibility that used QTL associated with pollen fertility and seed viability to identify loci that control fertility in interspecific crosses (Moyle and Graham, 2005). In another study, physical and genetic maps surrounding a major fruit weight QTL have been developed from isogenic lines derived from a *S. lycopersicum* × *S. pennellii* cross (Alpert and Tanksley, 1997; Frary et al., 2005). These maps may lead to a better understanding of the molecular biology of fruit development and to the genetic engineering of fruit size characteristics (Alpert and Tanksley, 1997; Frary et al., 2005). Introgression libraries are also being developed for *S.chmielewskii* and *S.lycopersicoides* (Chetelat and Meglic, 2000; Canady et al., 2005). QTL analysis strategies have found wide application in tomato studies by using breeding populations involving *S. pimpinellifolium*, *S. peruvianum*, *S. hirsutum* and *S. pennellii* (Ji and Scott, 2006).

3.1.5 Genetic linkage maps

65. Chetelat and Ji (2006) have recently reviewed the genetic linkage maps available for tomato. The first linkage map was developed for tomato consisted of classical morphological and isozyme markers (Stevens and Rick, 1986) and has since been revised by many authors. The first molecular linkage map was published by Tanksley et al. (1992) and has since been followed by numerous other maps. Fulton et al. (2002) used conserved ortholog set (COS) markers (markers derived from single-or low-copy genes conserved in two or more species that share common ancestry) to develop a new molecular linkage map. COS markers allow the development of linkage maps of plant genomes through comparative genetic maps, especially for species belonging to the same family, allow understanding of genome structure, and allow comparison of closely and distantly related species. The ability to detect single-copy orthologous genes among plant genomes has permitted comparative plant genomics to advance [for review, see Paterson et al., 2000) (Barone et al., 2009). Additional PCR-based anchor markers have been developed by Frary et al. (2005) that can facilitate mapping studies in tomato and related species.

66. The Solanaceae Genomics Network website (SGN) houses map and marker data for *Solanaceae* species as well as other genetic and mutagenesis in tomato populations (https://solgenomics.net/). Peralta et al. (2008) and Bedinger (2011) review the taxonomy, genetics, interspecific crossing barriers and breeding of tomatoes.

67. COS markers are genes that are conserved throughout evolution in both sequence and copy number (usually single or low copy) identified by comparative genomic studies involving two divergent species (tomato and Arabidopsis, Fulton et al., 2002). These genes may play roles that are essential to all plant species and can be used for comparative mapping, synteny and phylogenetic studies across the plant taxa. COS genes were further analysed and shortlisted to generate COSII markers which are PCR based markers developed from single copy, orthologous genes conserved across multiple species (tomato, potato, pepper, coffee and *Arabodopsis*; Wu et al., 2006). List of these markers and universal primers designed based on sequences of COSII gene are available at the SGN website.

SECTION IV - HYBRIDISATION AND INTROGRESSION

4.1. Breeding Tomato

68. Tomato (*Solanum lycopersicon*) has undergone intensive breeding for decades. Breeding and selection has been based on traits desirable for the processing or the fresh market. The processed market often involves growing tomatoes in open fields requiring simultaneous fruit ripening and machinery harvesting. In addition traits such as high sugar and total soluble solids content are required for the processed market. In the case of fresh market tomatoes, traits such as large fruit size, uniform fruit shape, uniform colour, long shelf life and fruit firmness are important (Menda and Mueller, 2013; Rick, 1978).

69. Over the last century, breeding and selection of tomatoes has resulted in numerous hybrids and cultivars. During the 1950s hybrid tomatoes were developed to obtain higher yields and improve fruit quality and disease resistance. Hybrids accounted for more than 50% of production both in protected cultivation, as well as in the open area. The production of hybrid tomatoes requires emasculation of flowers prior to cross-pollination. However, 40 male sterile mutants have been identified in tomato (Stevens and Rick, 1986) that can facilitate hybrid seed production. Marker assisted selection (MAS) is now a major instrument in conventional breeding. Markers linked to characteristics/traits of interest for breeding have been identified and developed for tomato (Ji and Scott, 2006).

70. *In vitro* culture and somatic hybridisation were also used in tomato breeding. Although all forms of S. *esculentum* var. *esculentum* are self-compatible and mainly inbreeding, the wild cherry tomato types have a tendency to outcross due to exsertion of the stigma beyond the anther cone at anthesis (Rick, 1950; McGuire and Rick, 1954). This may also happen to some degree in other *S. esculentum* forms through genetic control (Currence, 1944), resulting in changes to floral morphology (Rick, 1950) or adaptation to environmental conditions such as temperature (Howlett, 1939; Rick, 1950) and nutrients (Howlett, 1939). The domestication of the wild cherry tomato types (*S. esculentum* var. *cerasiforme*) in Mexico (Jenkins, 1948) eventually spread to Europe and by selection led to larger fruited varieties. It is believed that this selection also led to progressive shortening of the style and withdrawal of the stigma into the anther cone (Rick, 1950). This gave rise to the large-fruited self-compatible inbreeding varieties cultivated today (Rick, 1950). For this reason it is relatively easy to maintain a "true-to-type-variety" by saving their seed while not having to worry too much about outcrossing with other varieties of tomato. The several botanical varieties of tomato can be easily crossed with each other to produce viable offspring.

71. High fruit Total Soluble Solids (TSS) in tomatoes is a key component of fruit quality. TSS is a proxy for sugar content. Higher TSS increases consumer fruit likeability. Genetic, molecular and biochemical characterisation of wild tomato species with high fruit TSS (10–15% compared with 4–6% in cultivars) can be exploited in breeding programmes (Beckles et al., 2012). Nevertheless wild species with high TSS have low yield. An example of breeding a variety with both high TSS and yield is *Solara*.

72. Decades of breeding have resulted in a loss in genetic diversity. The challenges for breeders today include re-introducing the complex trait of flavour and breeding for novel disease resistance genes, that on average are effective for five years until the pathogen overcomes resistance (Menda et al., 2013). The wild species are the most valuable source of such traits.

4.2. Interspecific Crosses

73. In this section of the document the nomenclature used was the original that appears in each paper mentioned. The new names are not directly comparable with the previous ones (Table 1 and 2). The genus *Lycopersicon* has been divided into two subgenera based on their ability to cross with cultivated tomato. The *S. esculentum*-complex contains seven species that are easily crossed with cultivated tomato and these have served as a source of genetic variability for the improvement of tomato varieties (Rick, 1979). In contrast, the *L. peruvianum*-complex contains two species that are crossed with considerable difficulty (Stevens and Rick, 1986; Taylor, 1986), thus limiting the use of these species for tomato improvement. Nevertheless, gene flow between *L. peruvianum* and *L. chilense* has taken place to a limited extent and hybrids between species can be generated by grafting, if required (Städler et al., 2005). Hybridisation between these two subgenera usually leads to early embryo breakdown, which results in seed that is not viable. This problem can be circumvented by embryo culture and other laboratory techniques, albeit at great effort. Bedinger (2011) recently reviews interspecific reproductive barriers in the tomato clade. Table 5 summarises the breeding potential of *Lycopersicon.*

Table 5. **Breeding potential of *Lycopersicon***

Species	Mating System	Crossability with *L. esculentum*	Breeding use
***L. esculentum* complex**			
L. esculentum	Autogamous	Reciprocally compatible	Minor
L. pimpinellifolium	Mostly autogamous	Reciprocally compatible	Disease resistance Pest resistance Lycopene content
L. cheesmanii f. *cheesmanii*	Autogamous	Reciprocally compatible	Jointless pedicels High beta carotene Higher dry matter
L. cheesmanii f. *minor*	Autogamous	Reciprocally compatible	Salt and drought tolerance Disease resistance
L. parviflorum	Autogamous	Reciprocally compatible	Disease resistance
L. chmielewskii	Allogamous Self- compatible	Reciprocally compatible	Sucrose accumulation Disease tolerance
L. hirsutum f. *typicum*	Allogamous Self- incompatible	Unilaterally compatible	Cold tolerance
L. hirsutum f. *glabratum*	Self- compatible	Reciprocally compatible	Insect resistance Disease resistance Sucrose content
L. pennellii (*L. pennellii*)	Allogamous Self- compatible and self-incompatible biotypes	Unilaterally compatible	Drought tolerance Insect resistance Disease resistance
***L. peruvianum* complex**			

L. chilense	Allogamous Self- incompatible	Difficult Embryo rescue	Disease resistance Nematode resistance
L. peruvianum (L.) Mill.	Allogamous Self- incompatible	Very difficult Embryo rescue Bridge lines	Insect resistance Disease resistance Nematode resistance High sucrose content

Source: Taylor (1986) and Jones et al. (1993) with modifications.

4.2.1. L. pimpinellifolium, now S. pimpinellifolium

74. Some populations of this species differ considerably in morphology whereas others are highly uniform. Some populations are exclusively autogamous (self-pollinating) whereas others allow some outbreeding. This is due to exserted stigmas that project well beyond the anther cone (Rick, 1950). This species tends to readily cross as male parent with *L. esculentum* and is the only species to have exhibited a natural introgression with *L. esculentum*. In fact, it is probable that both species evolved from a common ancestor (Rick, 1950).

4.2.2. L. cheesmanii, now S. cheesmaniae

75. All forms of *L. cheesmanii* are self-compatible and are exclusively inbreeding. They can be hybridised with the cultivated tomato (*L. esculentum*).

4.2.3. L. parviflorum, now S. neorichii

76. This species is self-compatible and, due to floral morphology, is highly autogamous. *L. parviflorum* has an extremely small flower and the stigmas rarely protrude out of the anther cone. As a result, populations tend to be highly homozygous (Rick et al., 1976).

4.2.4. L. chmielewskii, now S. chmielewskii

77. This species is self-compatible. The flowers are large and very showy with long exerted stigmas. This seems to encourage outbreeding and, as a result, much variability is present in its population.

4.2.5. L. hirsutum, now S. habrochaites

78. *L. hirsutum* f. *typicum* is a strong outbreeder with a very long, exerted stigma. Most plant introductions are self-incompatible. Those that do self-fertilise produce weak progeny that suffer greatly from inbreeding depression. This form does not readily cross with *L. esculentum*. The other form, *L. hirsutum* f. *glabratum*, readily self-fertilises and progeny do not suffer from inbreeding depression. The latter form is also capable of crossing with *L. esculentum*. One of the first hybrid crosses was performed by Sawant (1958) to determine the relationships between *L. esculentum* and the two forms of *L. hirsutum*.

4.2.6. L. pennellii, now S. pennellii

79. This species can be readily crossed to *L. esculentum*. Both self-compatible and self-incompatible types exist. *L. pennellii* hybridises readily with cultivated forms and can also be crossed with

L. pimpinellifolium, *L. cheesmanii*, *L. parviflorum* and *L. hirsutum* but not with members of the *peruvianum* complex.

4.2.7. L. chilense, now S. chilense

80. This species is an obligate outbreeder. The first *L. chilense* x *L. esculentum* cross was performed and described by Holmes (1939). Crossing this species with the cultivated tomato is extremely difficult due to several barriers. The stigma of *L. chilense* will not accept pollen from the cultivated tomato and almost always leads to the abortion of the flower. The reciprocal cross, pollen from *L. chilense* applied to the stigma of *L. esculentum*, can result in the formation of fruit but few seeds are viable. However, some of the seeds do contain embryos of sufficient size to facilitate embryo rescue.

4.2.8. L. peruvianum, now S. peruvianum and S. corneliomulleri and S. arcanum

81. This species is exclusively an outbreeder. Crossing *L. peruvianum* with *L. esculentum* is rarely successful and attempts to cross these two species frequently result in embryo or flower abortion, even after the use of embryo rescue techniques (Hogenboom, 1972; Demirel and Seniz, 1997). To overcome this problem, Lanzhuang and Adachi (1996) developed an embryo culture method to obtain hybrid plants. Fortunately, these hybrids are capable of backcrossing to a *L. esculentum* parent (Kamal et al., 2001). Another method that has been successful at overcoming the incompatibility between the cultivated tomato and *L. peruvianum* is the use of *L. chilense* as a bridge species (*L. peruvianum* is crossed to *L. chilense* and that progeny is crossed to *L. esculentum*) (Poysa, 1990). Unfortunately this method often fails, but it does yield better results than a direct cross. A third method for crossing *L. peruvianum* and *L. esculentum* is the production of fertile somatic hybrids, with which backcrossing is possible (Kinsara et al., 1986).

4.2.9. Other species

82. The closest genetic relatives of tomato, *S. rickii* (Rick, 1988; DeVerna et al., 1990), *S. ochranthum* (Stommel, 2001), *S. juglandifolium* (Rick, 1988), *S. lycopersicoides* (Rick, 1951) and *S. sitiens* (Ji and Chetelat, 2004), are also crossable to *S. esculentum*. Chromosomal regions of *S. lycopersicoides and S. sitiens* have been introgressed into tomato (Pertuze et al., 2003; Canady et al., 2005).

4.3 Conservation of Genetic Diversity

83. The majority of the known improved varieties are related to the original fruit domesticated in Mesoamerica more than five hundred years ago. The most important changes introduced by the domestication process are: reduction of the gene pool, modification of the reproductive system and increase of fruit size. The gene pool characterising *Solanum lycopersicum* as a species has constantly been under human management. If this selection process diminishing genetic diversity continues, there is a risk of losing the genetic diversity that once gave rise to the original fruit.

84. As such, the breeding possibilities offered by using the knowledge of wild relatives of cultivated tomato are very diverse. At present, some characteristics of agricultural importance of tomato have been adapted based on the gene diversity present in wild relatives (Sánchez-Peña et al., 2004). As a result, diagnostic investigations and distribution studies of wild and weedy relatives present at the moment are a priority because of the high levels of genetic diversity they still preserve (Sim et al., 2012).

85. Bai and Lindhout (2007) presented the information about the genetic diversity collections in the Germplasm banks. This is mentioned in order to promote the conservation of the genetic diversity of tomato:

- The Germplasm Resources Information Network's (GRIN) www.ars-grin.gov
- Tomato Genetics Resource Center, in Davis, California. (TGRC http://tgrc.ucdavis.edu/)
- Botanical and Experimental Garden (http://www.bgard.science.ru.nl/)
- The Solanaceae Genome Network (http://zamir.sgn.cornell.edu/mutants/)

86. The contribution of Mesoamerica and the Andes area to the world does not only apply to the domesticated fruit, but also includes the amount of genetic information sheltered in the country's rural zones where domesticated crops, landraces and wild relatives coexist.

SECTION V - GENERAL INTERACTIONS WITH OTHER ORGANISMS (ECOLOGY)

87. Tomato plants compete with plant species or weed species for nutrients and resources. The broadleaf weeds and their control are the most important in tomato production. Examples of common problem weeds include velvetleaf (*Abutilon theophrasti*), redroot pigweed (*Amaranthus retroflexus*) and common lambsquarters (*Chenopodium album)*. Weed management involves the use of herbicides and inter-row cultivation (Robinson et al., 2006).

88. Weed species can also act as hosts for viruses and viral vectors. Two common weed species, lambsquarters (*Chenopodium album)* and cheeseweed (*Malva parviflora*) serve as hosts for both, an insect vector, the western flower thrip (*Frankliniella occidentalis),* and the tospovirus (tomato spotted wilt virus) it carries (Kahn et al., 2005).

89. Tomato plants are subject to attack by a variety of arthropods (listed in Appendix I) and this can result in yield losses. Tomato defence mechanisms against arthropod attack involve many factors, such as the chemical defenses of glandular trichomes and constituitive and wound-induced defences associated with leaf lamella (Kennedy, 2003). Glandular and non-glandular trichomes are found on the foliage and stems of *Lycopersicon* spp. Some varieties that utilise trichome–mediated defences, for example the wild species *L. hirsutum and L. pennelli*, are more resistant than others to insect attack. Certain glandular trichomes exude acylsugars that are toxic to several common tomato arthropod pests, including whiteflies, aphids, fruitworm, beet armyworm and agromyzid leafminer (Kennedy, 2003). In tomatoes, the jasmonic acid signal molecule is thought to represent an inducible plant defence to herbivory. Application of jasmonic acid induces proteinase inhibitors and polyphenol oxidases and decreases the abundance of many common herbivores, such as thrips, noctuid caterpillars and aphids (Thaler, 1999). Foliar tomato (*L.esculentum*) proteins, such as polyphenol oxidase, proteinase inhibitors and peroxidases, are differentially induced in response to herbivore attack (Stout et al., 1994). In plants, the jasmonic acid and salicylic acid (SA) signalling pathways can provide resistance to herbivore and pathogen attack and sometimes these pathways can interact. Interaction of these pathways in tomatoes results in reduced resistance of tomatoes to the herbivore, *Spodoptera exigua* and does not affect the bacterial pathogen, *Psuedomonas syringae pv. Tomato.* However, increased resistance to the bacterial pathogen is associated with SA activated responses (Thaler et al., 2002)

90. There are many microorganisms (bacteria, fungi and viruses) associated with tomato crops, some are beneficial while many represent pathogens of the tomato plant. Microbial pathogens are listed in Appendix II. The interactions between microorganisms, viruses, plants, and indeed, insect vectors is complex. For example, the bacterial endosymbiont (*Rickettsia* spp.) infects the sweet potato whitefly (*Bemisia tabacai*) and increases the transmission efficiency of the Tomato yellow leaf curl virus that the whitefly carries (Kliot et al., 2014).

91. Mycorrhizal fungi are ubiquitous soil microbes that form a symbiotic relationship with most terrestrial plants, and the largest group associated with most plant species are the vesicular-arbuscular mycorrhizal (VAM) fungi. VAM fungi interact with other microorganisms such as plant-growth–promoting rhizobacteria. VAM colonised roots of tomato plants were found to attract higher levels of the rhizobacteria - *Azotobacter* and *Psuedomonas flourescens* in comparison to non-VAM tomato roots (Sood, 2003). Other beneficial plant growth promoting bacteria and fungi include *Pseudamonas flourescens* and

Glomus mosseae which increase plant mineral nutrition by increasing leaf phosphorus content (Gamalero et al., 2004). Some plant growth promoting rhizobacteria can exhibit antagonism towards some of the most common soil-borne root pathogens of tomato such as *Fusarium oxysporum f. sp. radices-lycopersici*, *Pythium ultimum, Rhizoctonia solani* and *Pyrenochaeta lycopersici*. In particular antagonism is associated with siderophore producers (De Brito et al., 1995).

92. Microorganisms isolated from the rhizosphere of tomato plants, were examined and two species, a bacterial species (*Pseudamonas putida*) and a fungal species (*Tricoderma viride*) demonstrated plant growth-promoting activity on greenhouse tomato plants grown under a hydroponic system. Plant growth promotion is thought to be mediated through the production of indole acetic acid (IAA) by the microorganisms (Gravel et al., 2007).

SECTION VI - HUMAN HEALTH AND BIOSAFETY

93. Tomato is widely consumed worldwide. Tomato is a popular species preferred in gastronomy for its characteristic flavour. It is used in several traditional dishes because of the compatibility with other food ingredients and high nutritional value (OECD, 2008). The many end uses of tomato fruit, as well as food and feed safety considerations (including composition of key food and feed nutrients, anti-nutrients, allergens, and toxicants) are detailed in the OECD Consensus Document on Compositional Considerations for New Varieties of Tomato (2008).

APPENDIX I - TOMATO PESTS

Insects

Some of the most important insect pests of tomato are the following:

Scientific Name	Common Name	Virus Transmitted
Bemisia argentifolii Bellows and Perring	Silverleaf whitefly	TYLCV
Circulifer tenellus Baker	Beet leafhopper	CTV, BLTVA
Epitrix hirtipennis Melsheimer	Flea beetles	None
Frankliniella bispinosa Morgan	Florida flower thrip	TSWV, TSV
Frankliniella fusca Hinds	Tobacco thrip	TSWV, TSV
Frankliniella occidentalis Pergande	Western flower thrip	TSWV, TSV
Frankliniella shultzei Trybom	Common blossom thrip	TSWV, TSV
Heliothis armigera Hübner / *H. zea* Boddie	Fruit worms	None
Keiferia lycopersicella Wallshingham	Tomato pinworm	None
Leptinotarse decemlineata Say	Colorado potato beetle	None
Lygus ssp. Hahn	Lygus bugs	None
Lyriomyza trifolii Burguess	Vegetable leafminer	None
Manduca sexta L. / *M. quinquemaculata* Havorth	Tobacco and tomato hornworms	None
Nezara viridula L.	Southern stink green bug	None
Peridroma saucia Hübner *Agrotis ipsilon* Hufnagel	Variegated cutworm Black cutworm	None
Phthorimaea operculella Zeller	Potato tuberworm	None
Scutigerella immaculate ssp. Newport	Garden symphlyans	None
Spodoptera exigua Hübner	Beet armyworm	None
Thrips tabaci Lindeman	Onion thrip	TSWV, TSV
Trialeurodes vaporariorum Westwood	Greenhouse whitefly	Tomato Infectious Chlorosis Virus
Trichoplusia ni Hübner *Trioza* spp. *Tuta absoluta* Meyrick	Cabbage looper Tomato psyllid Micro lepidoptiron moth	None
Various species	Aphids	AMV, CMV, TEV

Mites

Some of the most important mite pests of tomato are the following:

Scientific Name	Common Name	Virus Transmitted
Aculops lycopersici Massee	Tomato russet mite	None
Polyphagotarsonemus latus Banks	Broad mite	None

Nematodes

Some of the most important nematodes of tomato are the following:

Scientific Name	Common Name	Virus Transmitted
Meloidogyne ssp. Göldi *Meloidogyne enterolobii*	Root knot nematodes	None
Xiphinema americanum Cobb	American dagger nematode	TRSV
Rotylenchulus reniformis Lindfor and Oliveira	Reniform nematode	None

APPENDIX II - TOMATO DISEASES

The following lists include the most relevant diseases in terms of economic losses.

Bacteria

Scientific Name	Common Name
Clavibacter michiganense Smith	Bacterial canker
Pseudomonas corrugate Roberts & Scarlett	Tomato pith necrosis
Ralstonia (Pseudomonas) solanacearum Smith	Bacterial wilt
Pseudomonas syringae van Hall pv. *tomato*	Bacterial speck
Xanthomonas campestris Pammel	Bacterial spot

Oomycetes and Fungi

Scientific Name	Common Name
Alternaria alternate (Fries) Keissler	Tomato black mold
Alternaria alternata f. sp.l*ycopersici* Grogan et al.	Alternaria stem canker
Alternaria solani (Ell.& Mart.) Jones & Grout.	Early blight
Botrytis cinerea	Gray mold
Cladosporium fulvum	Leaf mould
Colletotrichum Ssp. Cordá	Anthracnose
Fusarium oxysporum f. sp.l*ycopersici* Vawdrey & Peterson	Fusarium wilt
Fusarium oxysporum f. sp. *radicis-lycopersici* Jarvis & Shoemaker	Tomato Fusarium crown and root rot
Fusarium solani (Mart.) Sacc.	Tomato Fusarium foot rot
Leveillula taurica(Lev.) Arnaud syn. *Oidiopsis taurica* Salmon	Tomato powdery mildew
Phytium ultimum Trow	Tomato water mold
Phytophthora parasitica Dastur and *P. capsici* Leonian	Tomato Phytophthora root rot
Phytophtora infestans (Mont.) de Bary	Late blight
Pyrenochaeta lycopersici Schneider & Gerlach	Tomato corky root rot
Sclerotinia sclerotiorum (Lib.) de Bary	Tomato white mold
Sclerotium rolfsii Sacc.	Tomato southern blight
Verticillium albo-atrum Reinke & Berthold and *V. dahlia* Kleb.	Verticillium wilt

Viruses

Common Name	Acronym
Alfalfa Mosaic Virus	AMV
Cucumber Mosaic Virus	CMV
Potato Virus Y	PVY
Tobacco Etch Virus	TEV
Tobacco Mosaic Virus	TMV
Tobacco Streak Virus	TSV
Tomato Big Bud or Beet Leafhopper Transmitted Viresence Agent	BLTVA
Tomato Bushy Stunt Virus	TBSV
Tomato Infectious Chlorosis Virus	
Tomato Mosaic Virus	ToMV
Tomato or Beet Curly Top Virus	CTV
Tomato Ringspot Virus	TRSV
Tomato Spotted Wilt Virus	TSWV
Tomato Yellow Leaf Curl Virus	TYLCV
Tomato golden mosaic begomovirus	TGM
Tomato Pepper Huasteco begomovirus	TPH
Peanut Bud Necrosis tospovirus	PBN

APPENDIX III - BIOTECHNOLOGICAL DEVELOPMENTS

94. At present, great efforts of biotechnology in tomatoes have focused on the resistance against diseases caused by fungi, bacteria and viruses as well as on the tolerance to stress and pesticide exposure. In some cases, tomato plants are bred for development of varieties having increased nutritional or health benefits (Herbers, 2003).

95. The wealth of molecular biology research for tomato and the availability of efficient transformation protocols have made this crop species a highly attractive target for genetic manipulation. Indeed, the first product from a transgenic plant released and approved for human consumption was a transgenic tomato line called “Flavr Savr” which had delayed ripening properties. Flavr Savr was developed in 1994 by Calgene Company (Herrera and Martínez-Trujillo, 2005; Llop-Tous et al., 2000; Bird et al., 1988), but was later withdrawn from the market due to the poorly adapted germplasm used at the early stage of biotech development. Subsequently in 1995, a genetically modified tomato was produced by Zeneca with similar properties. This product is available nowadays on the market as a processed product, tomato purée (Herrera and Martínez-Trujillo, 2005). In addition to fruit ripening characteristics, other potential targets of tomato gene manipulation are as follows:

Fruit quality**:** Fruit ripening research discovered that the enzyme polygalacturonase (PG) is responsible for the degradation of pectin (which maintains the unity of the cell walls), causing subsequent softening of the fruit. The PG gene synthesising this enzyme was identified in order to block or delay its production without altering other ripening mechanisms and to extend shelf life of the fruit (Herrera and Martínez-Trujillo, 2005; Bird, 1988). Both Flavr Savr and the variety developed by Zeneca manipulated this gene. Another development was the suppression of the formation of the ripening hormone ethylene, by suppressing the enzymes (ACC synthase and ACC oxidase) involved in ethylene production or by metabolising ethylene precursors; SAM and ACC by expressing enzymes like SAM hydrolase and ACC deaminase.

Virus resistance**:** Disease resistance is one of the most thoroughly explored branches of genetic engineering. In the case of tomato, viruses are devastating phytopathogenic agents. For example, the pepino mosaic virus is a major disease of tomatoes grown in greenhouses worldwide (Cottilon et al., 2002; French et al., 2001; Hanssen et al., 2010; Ling, 2007; Ling and Scott, 2007; Maroon-Lango et al., 2005; Mumford and Metcalfe, 2001; Pagán et al., 2006; Van der Vlugt et al., 2000). At present plant lines resistant to tobacco mosaic virus have been developed by adding the gene *Tm*. Several aspects regarding the interaction of a resistance gene product and a viral-encoded protein have been identified as well. This is particularly the case for recessive resistance genes operating against potyviruses, although the exact mechanism which inhibits virus infection is still not clear (Palukaitis and Carr, 2008; Palukaitis et al., 2008; Piron et al., 2010).

Disease resistance**:** Fungi cause great losses in tomato cultivation. Transgenic tomatoes resistant to *Fusarium* attacks were developed by the identification of two genes which code for enzymes that degrade the most important components of fungal cell walls (chitin and beta-1-3-glucan) (Tammeling et al., 2002). The tomato *Pto* gene confers resistance to races of *Pseudomonas syringae* pv. *tomato* that carry the *avrPto* gene (Martin et al., 1993; Hammond-Kosack and Jones, 1997). Resistance to the leaf mould pathogen *Cladosporium fulvum* is conferred by distinct *Cf* genes, which have been introgressed from various wild *Solanum* species or landraces into

cultivated tomato *S. lycopersicum* (Dixon et al., 1996). The gene *Mi*, which confers resistance to several species of root-knot nematode, is present in many modern tomato cultivars (Jacquet et al., 2005; Sorribás et al., 2005; Williamson, 1998).

Insect resistance: Open field grown tomatoes suffer from Lepidopteran attacks. Genes from *Bacillus thuringiensis* (Bt) bacteria have been used to create plants resistant to those attacks. Certain Bt genes encode crystalline enzymes with insecticidal effect (delta endotoxins). As their activity is taxon specific (for example, the “Cry lll” protein only affect beetles), specialised transgenic plants have been generated that are resistant to specific insect attacks (Collinge et al., 2007; Herrera and Martínez-Trujillo, 2005; Fillatti et al., 1987). The expression of δ-endotoxins in transgenic plants has provided a very effective means to control economically important insect pests in order to overcome the instability and degradation of *Cry* proteins when exposed to ultraviolet radiation and short persistence on the plant.

Resistance/tolerance to abiotic stress**:** In order to increase the geographical range in which tomato can be grown, research is being undertaken to produce transgenic tomato lines resistant to drought, low temperatures and salinity. This would allow the transgenic plants to grow, flower and produce fruits in habitats with high levels of salinity (200mM). Moreover, they also preserve fruit quality with low sodium content (Herrera and Martínez-Trujillo, 2005, Goel et al., 2010).

Vaccine production**:** Tomato has been used as a host system to produce a number of vaccines: plague, SARS, *E. coli*, Hepatitis, HIV, Alzheimers, Enterovirus 71, RSV, Malaria and Cholera. A number of these transgenic fruits have been tested on laboratory animals shown to induce an immune response, indicating a potential for the development of human vaccines (Youm et al., 2008; Denis et al., 2007; Alvarez et al., 2006). The results indicate that tomato plants may provide a useful system for the production of human Ab antigen (Youm et al., 2008; Lou et al., 2007).

Anthocyanin accumulation in tomato**:** In view of the presumed beneficial effect of plants antioxidants to human health several research groups have investigated the possibility of increasing the antioxidant levels in tomato fruit through transgenic approaches. Positive results have been obtained for carotenoides (Davuluri et al., 2005; Fraser et al., 2007), phenylpropanoids and specially polyphenols (Muir et al., 2001; Bovy et al., 2002; Verhoeyen et al., 2002; Davuluri et al., 2005; Schijlen et al., 2006; Butelli et al., 2008)

Table 6. **Approved GM events for modified product quality in Tomato**

GM Traits	Event	Name	Developer
Events with Delayed ripening/senescence	1345-4	----------	DNA Plant Technology Corporation (USA)
Events with Delayed ripening/senescence	35-1-N	-----------	Agritope, INC, USA
Events with Delayed ripening/senescence	8338	CGN-89322-3	Monsanto Company
Events with Delayed ripening/senescence	Huafan-1	------------	Huazhong Agricultural University (China)
Lepidopteran insect resistance	5345	-----------	Monsanto Company
Antibiotic resistance	B	SYN -0000B6	Zeneca Plant Science and Petoseed Company
Antibiotic resistance	DA Dong No.9	SYN-000DA-9	Zeneca Plant Science and Petoseed Company
Antibiotic resistance	F (1401F, h38F, 11013F, 7913F)	SYN-0000F-1	Zeneca Plant Science and Petoseed Company
Events with Delayed ripening/Antibiotic resistance	FLAVR SAVR	CGN-89564-2	Monsanto Company
Viral disease resistance	PK-TM8805R	---------------	Beijing University
Novel tomato flavour	--------------	*Del Ros1*	Butelli et al., 2008

Source: ISAAA, GM Approval Database www.isaaa.org/gmapprovaldatabase

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