



The Tomato Collection Maintained by AVRDC – The World Vegetable Center: Composition, Germplasm Dissemination and Use in Breeding

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Abstract

With about 82,400 accessions, the section *Lycopersicon* in the genus *Solanum* is well represented in *ex situ* collections around the globe. The single largest collection (approximately 10% of total global resources) is held by AVRDC – The World Vegetable Center in Taiwan, followed by genebanks in the United States, the Philippines, Germany, the Russian Federation, and Japan. AVRDC's tomato collection is composed of cultivated tomato (6,142 *S. lycopersicum* accessions—mostly traditional cultivars and landraces, and 125 *S. lycopersicum* var. *cerasiforme* accessions), crop wild relatives (812 accessions), and genetic stocks (595 accessions) composed of interspecific hybrids, introgressed lines, and recombinant inbred lines. A total of 585 accessions still lack proper species identification. After pepper (*Capsicum* spp.), tomato is AVRDC's second most widely distributed vegetable crop. Wild relatives of tomato have been crucial in the improvement of pest and disease resistance and abiotic stress tolerance of cultivated tomato through classical breeding. Virtually all significant resistance genes to tomato diseases were sourced from wild relatives. Research work at AVRDC has focused on the introduction of resistance genes into cultivated tomato against late blight, bacterial wilt and leaf curl (caused by begomoviruses) and the development of heat-tolerant lines. Since 1978, 180 tomato cultivars have been released in 45 countries worldwide based on AVRDC-developed open-pollinated, heat-tolerant and multiple disease-resistant germplasm. In addition, nine commercial tomato lines have been released by seed companies in India using AVRDC breeding lines as parent material in the development of hybrids. This success was possible due to the genetic building blocks conserved in AVRDC's diverse tomato collection.

INTRODUCTION

In economic terms, tomatoes are a very important vegetable crop and widely grown in 175 countries (FAOSTAT, 2014). Tomato ranked second in terms of global production among 27 vegetable and melon commodity groups grown worldwide in 2012, with an output of 161.8 million tons and a net production value of 59.1 million international dollars (FAOSTAT, 2014). China was by far the largest producer of this commodity (50 million tons; 30.9% of world production), followed by India (17.5 million tons; 10.8%), and the United States (13.2 million tons; 8.2%). During the last 22 years (1991-2012) the tomato production area expanded from 2.86 to 4.8 million hectares



(67.8% increase), yield increased from 26.6 to 33.7 t/ha (26.6% increase), and production quantity more than doubled from 76.1 to 161.8 million tons (FAOSTAT, 2014).

CENTER OF ORIGIN AND DOMESTICATION, TAXONOMY AND WILD RELATIVES OF TOMATOES

Cultivated tomatoes (*Solanum lycopersicum* L.) belong to the Solanaceae family, which comprises 95 accepted genera (USDA-ARS, 2014). Among those 95 genera, *Solanum* is by far the largest and most diverse genus in this family, comprising 1,000 to 2,000 species (Knapp, 2002). Despite being very diverse and covering a wide range of habitats—from rainforests to the world's driest deserts—the genus *Solanum* is cytogenetically very conservative and most taxa have a basic chromosome number of $n=12$ (Chiarini et al., 2010).

Botanically classified as a berry, tomatoes originated in the South American Andes, ranging from northern Chile in the south, through Bolivia, Peru to Ecuador and Colombia in the north (Grubben and Denton, 2004; Bai and Lindhout, 2007). Initially, Peru had been proposed as the center of domestication of tomato, thus coinciding with its center of origin and genetic diversity. However, genetic evidence points to Mexico as the center of domestication, as modern cultivars appear to be closely related to a cherry tomato-like cultivar grown widely in Mexico and throughout Central America at the time of discovery by the Spanish (Rick, 1995). The cherry tomato (*S. lycopersicum* L. var. *cerasiforme* (Dunal) D.M. Spooner et al.) is thought to be the direct ancestor of cultivated tomato (Tanksley, 2004) and this botanical variety is still found in a semi-wild state in Central America.

The generic status of tomato has been in flux since the 16th century, and has changed several times, from *Solanum* to *Lycopersicon* and back again to *Solanum*. Today, there is a general acceptance by both taxonomists and breeders to describe tomato in the section *Lycopersicon* under the genus *Solanum*. This decision is based on evidence derived from phylogenetic studies using DNA sequences and more in-depth studies of plant morphology and distribution of the species (Peralta et al., 2006). The section *Lycopersicon* in the genus *Solanum* comprises only one domesticated species, *S. lycopersicum* L. (Tanksley, 2004) and 12 crop wild relatives (Peralta et al., 2006; Bai and Lindhout, 2007). The currently known 13 tomato species have been grouped into the *Solanum lycopersicum* and the *S. peruvianum* complex (Peralta et al., 2006; Ebert, 2013).

Most species within the *S. lycopersicum* complex can reciprocally hybridize with cultivated tomato, with the exception of *S. habrochaites* (Robertson and Labate, 2007). *S. habrochaites* can act as a pollen parent in crosses with cultivated tomato, but the reciprocal cross does not set fruit.

Within the *S. peruvianum* complex, compatibility with cultivated tomato is rather limited. *S. chilense* can act as a pollen parent for *S. lycopersicum*, but viable seeds are rare and embryo rescue is required (Robertson and Labate, 2007). *S. chilense* does not accept pollen from the cultigen in a reciprocal cross. *S. peruvianum* is the most widespread and genetically and morphologically most diverse species within the section *Lycopersicon* (Peralta et al., 2005), but presents severe crossing barriers in hybridization attempts with cultivated tomato (Robertson and Labate, 2007). Two new wild species, *S. huaylasense* and *S. arcanum* have only recently been described (Peralta et al., 2005). *S. huaylasense* is endemic in northern Peru at an elevation of 1,700 to 3,000 m. *S. arcanum* is also found in



northern Peru, but at lower elevations from 100 m in coastal and inland Andean valleys up to 2,800 m on ridges, dry valleys and dry rocky slopes (Peralta et al., 2005). There is considerable intraspecific variation in *S. arcanum*, which led to the description of four morphotypes.

The domestication and transmigration process of tomato from the Andes to Central America and from there to Europe caused a major genetic drift in this inbreeding crop. It has been reported that the genomes of cultivated tomato contain less than 5% of the genetic diversity of their wild relatives (Miller and Tanksley, 1990). Despite this narrow genetic base, cultivated tomato is extremely rich in shapes, colors and sizes, in contrast to the wild forms which bear only tiny fruit. It is likely that mutations associated with larger fruit were selected and accumulated during tomato domestication (Bai and Lindhout, 2007). The genetic potential of wild tomato relatives became apparent only in the 20th century when Charles Rick made initial crosses between wild and cultivated tomato. Interspecific crosses are now widely used by tomato breeders to tap into the gene pool of wild tomato relatives when breeding for resistance to biotic and tolerance to abiotic stresses.

TOMATO GERMPLASM HOLDINGS WORLDWIDE AND COMPOSITION OF AVRDC'S COLLECTION

The section *Lycopersicon* in the genus *Solanum* is well represented in genebanks around the globe with 82,393 germplasm accessions kept *ex situ* (Table 1). The largest individual collection in the public sector (8,259 accessions; 10% of world holdings) is held by AVRDC in Taiwan, followed by genebanks in the US, the Philippines, Germany, the Russian Federation, Japan, Canada, Colombia, Spain, and India.

The tomato collection of AVRDC is composed of 6,142 *S. lycopersicum* accessions—mostly traditional cultivars and landraces, 125 *S. lycopersicum* var. *cerasiforme* accessions, 812 accessions of wild tomato relatives, 585 accessions with still-unidentified species name, and a total of 595 hybrids, introgression lines (ILs), and recombinant inbred lines (RILs) (see Ebert, 2013 for more details). The following countries made major contributions to AVRDC's collection of cultivated tomato: US (1,197 accessions), China (453), El Salvador (411), Taiwan (394), Peru (305), Guatemala (231), the Philippines (217), Turkey (194), India (152) and Hungary (149).

Compared with interspecific hybrids, ILs and RILs are much more useful for quantitative trait loci (QTL) identification as they carry a single introgressed region in the genome of the cultivated species. This avoids bias due to epistasis commonly inherent in mapping populations derived from different species (Lippman et al., 2007). Phenotypic variation in the ILs can be linked with individual introgression segments. This allows the pyramiding of various quantitative traits from different ILs into new breeding lines to maximize yield, resistance to diseases (Vidavski et al., 2008; Hanson et al., 2012), and tolerance to abiotic stress.

Among AVRDC's wild tomatoes, the *S. pimpinellifolium* collection is the largest one and comprises 330 accessions. To facilitate the use of *S. pimpinellifolium*, which can be easily crossed with cultivated tomato, AVRDC research staff established a core collection composed of 75 accessions representing 22.7% of AVRDC's entire *S. pimpinellifolium* collection (Rao et al., 2012). It is a well-balanced core with a good representation of the different populations identified in the study as well as their



geographic origins, with 40 accessions from Peru, 17 from Ecuador, 14 from Mexico and 4 from other countries.

USE OF TOMATO GERMPLASM FOR BREEDING AT AVRDC

Soon after the creation of AVRDC in 1971, the Center assembled a modest collection of 590 accessions of three crop groups: Brassicas, tomato and *Vigna*, with the aim of developing crop varieties able to perform well under tropical conditions. Insect pests, diseases, high temperatures, salinity and drought limit yield of vegetable crops under tropical and subtropical conditions. Tomato yields in sub-Saharan Africa and tropical Asia are only 10-12 t/ha (Hanson et al., 2012) compared with 33.7 t/ha worldwide (FAOSTAT, 2014).

Since its inception, a major aim of the AVRDC tomato breeding program has been the increase of yield in hot-wet and hot-dry tropical environments. Tomato fruit set is favored at mean temperatures of 21-24 °C and declines as mean temperatures rise above 25 °C (de la Peña et al., 2011). High temperatures adversely affect fruit setting at all stages, including flower and gamete formation, anther development, pollination and fertilization, and fruit development (Peet et al., 1998). In addition to reduced fruit set, high temperatures reduce fruit weight and impair fruit quality, including poor color development and increased incidences of fruit cracking, blossom-end rot and other fruit defects.

Hence, a major effort of the initial AVRDC tomato breeding program was to increase heat tolerance and to incorporate genes for multiple disease resistance in the humid tropics. For this purpose, diverse germplasm was acquired and evaluated for the desired traits. Initial screening trials for heat tolerance led to the identification of 31 out of 3799 accessions that set abundant fruit at temperatures above 22 °C (AVRDC, 1975). Surprisingly, the source of heat tolerance was not exclusively restricted to the tropics. Four tolerant lines originated from Canada, two from the United Kingdom, four from Hungary and three from the US. About half of the heat-tolerant accessions did come from tropical countries (AVRDC, 1975). As the search for heat tolerance continued, new lines that produced up to 70% of normal fruit set at 29°-31 °C night temperatures were identified (Fletcher, 1993).

Opeña et al. (1988) reported 11 tomato diseases that are important in the hot and humid tropics: bacterial wilt (*Ralstonia solanacearum*), root-knot nematode (*Meloidogyne incognita*), Tomato mosaic virus, leaf mold (*Cladosporium fulvum*), grey leaf spot (*Stemphylium solani*), Septoria leaf spot (*Septoria lycopersici*), southern blight (*Sclerotium rolfsii*), early blight (*Alternaria solani*), late blight (*Phytophthora infestans*), powdery mildew (*Erysiphe polygoni*, *Leveillula taurica*), and bacterial spot (*Xanthomonas campestris* pv. *vesicatoria*). Among them, bacterial wilt had the highest priority at the start of the tomato breeding program of AVRDC (Opeña et al., 1988) and continues to be a major focus of AVRDC's current research efforts due to its destructive effects under hot-wet growing conditions (Wang et al., 2013).

Another major tomato disease in the tropics and subtropics is tomato yellow leaf curl disease. Periods of warm and dry conditions favor rapid increase of whiteflies (*Bemisia tabaci*), which transmit begomoviruses that cause the disease. Early begomovirus infections of susceptible varieties result in severe stunting, foliar chlorosis and losses of commercial yield that can reach up to 100% (Hanson et al., 2012).



Wild relatives of tomato have been crucial in the improvement of pest and disease resistance and abiotic stress tolerance of cultivated tomato through classical breeding. Virtually all significant resistance genes to tomato diseases were sourced from wild relatives. Research work at AVRDC has focused on the introduction of resistance genes into cultivated tomato against late blight, bacterial wilt and tomato yellow leaf curl. Accessions of *S. chilense*, *S. peruvianum*, and *S. habrochaites* have shown high levels of resistance to tomato yellow leaf curl. Interspecific crosses and backcrosses have led to the introgression of *Tomato yellow leaf curl virus* (TYLCV) resistance genes *Ty-1*, *Ty-2*, *Ty-3*, *Ty-4* and *Ty-5* into cultivated tomato (Ji et al., 2007; Anbinder et al., 2009). AVRDC field trials in Taiwan under high tomato yellow leaf curl pressure showed that combinations of *Ty-1+Ty-2+Ty-3*, *Ty-1+Ty-3*, or *Ty-2+Ty-3* out-yielded the susceptible check nine-fold (Hanson et al., 2012).

The availability of single major resistance genes, many of them with dominant inheritance, has made classical disease resistance breeding in tomato quite successful. In contrast, plant response to environmental stress is highly influenced by environmental variation and, in general, is quantitatively inherited, involving many genes. Salinity is an increasingly important environmental constraint to crop production in arid and semi-arid regions and coastal areas. While genetic variability for salt tolerance traits is limited in cultivated tomato, sources of tolerance have been reported in several wild tomato species, among them *S. pimpinellifolium*. A sub-set of AVRDC's *S. pimpinellifolium* accessions was screened for salinity tolerance under progressive salt stress until a final electrical conductivity (EC) of 40 dS/m was reached (Rao et al., 2013). Five genotypes (4 belonging to the core collection) were identified with good survival traits, seven with superior yield traits, and two with combined good survival and yield traits under salt stress.

TOMATO GERMPLASM DESSIMINATION BY AVRDC – THE WORLD VEGETABLE CENTER

After pepper, tomato is AVRDC's second most widely distributed vegetable crop. During the last 13 years (2001-2013) a total of 22,258 germplasm samples were distributed from headquarters to 138 countries worldwide (Fig. 1). The majority of the distributed samples (22,258; 81%) were improved lines developed by AVRDC breeders, while 5,180 samples (19%) were genebank accessions. This ratio is very similar to the dissemination of pepper germplasm over the last 12 years as described by Lin and co-workers (2013). With the exception of the US and the Netherlands, only Asian countries were among the top ten recipient countries. This might be attributable to the fact that AVRDC had a clear focus on Asia during the first 20 years of its existence, after which it expanded its range of activities to sub-Saharan Africa and other parts of the world.

It is also interesting to note that the top three tomato-producing countries in the world (China, India, and the US) were among the top four tomato germplasm recipient countries—an indication of the relevance of AVRDC tomato germplasm for the top producing countries. A total of 10,896 germplasm samples (39.7% of total) were shipped to 128 other countries (Fig. 1). Most countries preferred to receive improved lines developed by AVRDC, except Japan, Taiwan, and Pakistan, where the share of genebank accessions clearly dominated and reached 81.8%, 37.7% and 60.6%, respectively. The Netherlands also had a relatively high share of genebank accessions, at 41.5%. A



relatively high demand of genebank accessions compared with improved lines is an indication that there are strong private and/or public tomato breeding programs in those countries that can exploit the full potential of the genetic variability of germplasm accessions. Government organizations, seed companies and universities were the top three recipient categories of AVRDC tomato germplasm (Fig. 2).

Since 1978, 180 tomato cultivars have been released in 45 countries worldwide based on AVRDC-developed open-pollinated, heat-tolerant and multiple disease-resistant germplasm. In addition, nine commercial tomato lines have been released by seed companies in India using AVRDC breeding lines as parent material in hybrid development. This success was possible due to the genetic building blocks conserved in AVRDC's diverse tomato collection.

CONCLUSION

Tomato is a priority crop at AVRDC, in line with the importance of this vegetable worldwide. The Center maintains the single largest tomato germplasm collection in the public domain and breeders have worked since the foundation of the Center on the development of improved varieties for good adaptation to tropical and subtropical conditions to support small-scale farmers in developing countries. Diseases, insect pests and abiotic stress threaten the crop, especially under tropical climates. Breeders must cope with these biotic and abiotic challenges, which increasingly are exacerbated by the changing climate. Mobilization and use of the genetic diversity available in the wild gene pool will allow breeders to adapt cultigens to rapidly changing environmental conditions and boost agricultural production to ensure food and nutrition security.

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Tables

Table 1. Major tomato germplasm collections held by selected genebanks worldwide.

| Genebank | | | Accessions | |
|----------------|-------------------------------|--------------------|--------------------|-------------|
| Institute code | Acronym | Country | No. | Percent (%) |
| TWN001 | AVRDC | Taiwan | 8,259 ¹ | 10 |
| USA003 | NE9 | USA | 6,343 | 8 |
| USA094 | DHSNYST | USA | 4,850 | 6 |
| PHL130 | IPB-UPLB | Philippines | 4,751 | 6 |
| USA117 | Campbell Inst. Agric. Res. | USA | 4,572 | 6 |
| DEU146 | IPK | Germany | 4,063 | 5 |
| USA176 | GSLY | USA | 3,395 | 4 |
| RUS001 | VIR | Russian Federation | 2,540 | 3 |
| JPN003 | NIAS | Japan | 2,428 | 3 |
| CAN004 | PGRC | Canada | 2,137 | 3 |
| COL004 | ICA/REGION 5 | Colombia | 2,018 | 2 |
| ESP026 | BGUPV | Spain | 1,928 | 2 |
| IND001 | NBPGR | India | 1,788 | 2 |
| | Others (148) | Others | 33,321 | 40 |
| | Total | World | 82,393 | 100 |

¹Actual data (June 2014) from Asian Vegetable Genetic Resources Information System (AVGRIS)



Source: Derived from data supplied by the WIEWS database, consulted on 9 July 2014 (WIEWS, 2014) http://apps3.fao.org/wiews/wiews.jsp?i_l=EN.

Figures

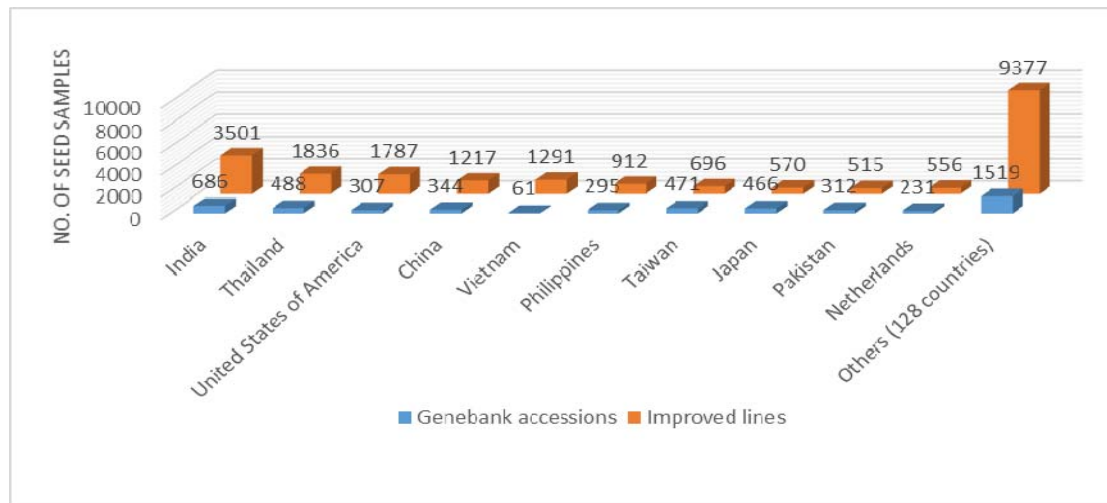


Fig. 1. Worldwide tomato seed distribution by AVRDC – The World Vegetable Center during the period 2001 to 2013 (top 10 recipient countries listed). Total: 27,438 seed samples, out of which 5,180 were samples of genebank accessions and 22,258 were samples of improved lines.

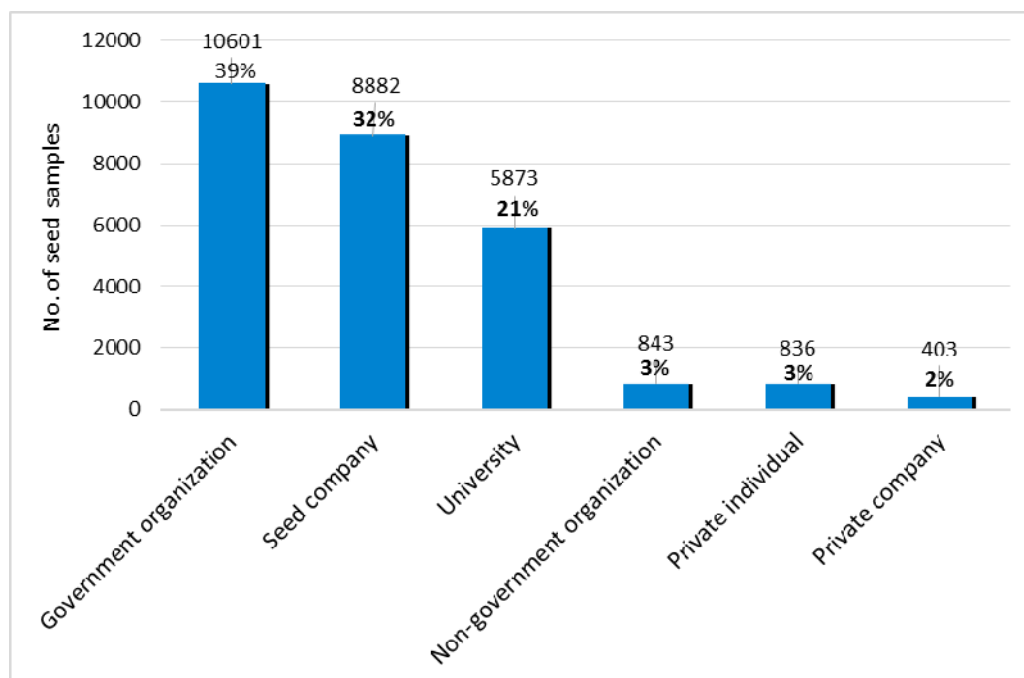


Fig. 2. Worldwide tomato seed distribution by AVRDC – The World Vegetable Center during the period 2001 to 2013 by recipient category.