



# Cuticular hydrocarbons and sucrose esters as chemotaxonomic markers of wild and cultivated tomato species (*Solanum* section *Lycopersicon*)



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## ARTICLE INFO

### Article history:

Received 19 May 2016

Received in revised form

1 September 2016

Accepted 29 September 2016

Available online 4 October 2016

### Keywords:

*Solanum lycopersicum* L.

*Solanum pennellii* Correll

Solanaceae

Tomato

Chemotaxonomy

Cuticular hydrocarbons

Sucrose esters

## ABSTRACT

The tomato (*Solanum lycopersicum* L.) is one of the most important vegetables worldwide. Due to the limited genetic variability, wild related species are considered as potential gene pool for breeding cultivated plants with enriched genetic basis. Taxonomic relations between tomato species at the level of single groups and taxa still remain, however, not fully resolved. Hence, in addition to already reported classification based on the morphology of the plants and molecular markers, we proposed chemotaxonomic approach to unveil some aspects of tomato taxonomy.

Cuticular hydrocarbons and surface sucrose esters (SEs) were used as chemotaxonomic markers. Classification based on the cuticular hydrocarbon profile was in good agreement with other taxonomic studies as long as between-species differences were taken into account. Clear separation of the common tomato and closely related species from the majority of *S. pennellii* accessions was obtained. In the same time, however, *S. pennellii* revealed broad variation: based on the results, three highly distinct types of these plants were proposed, among them one type was very similar to cultivated tomato and its relatives. Addition of SEs profiles to the dataset did not impair the classification, but clarified the position of *S. pennellii*. The results suggest possible hybrid origin of some of *S. pennellii* and wild *S. lycopersicum* accessions, and the approach proposed has a potential to identify such hybrid plant lines.

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## 1. Introduction

Historically, tomato species were usually classified within the genus *Lycopersicon*; sometimes, however, they were also placed in *Solanum* genus (Peralta and Spooner, 2000). The majority of taxonomists initially agreed with the former classification: first more recent taxonomic treatments of tomatoes by Müller (1940) and Luckwill (1943) described *Lycopersicon* as a distinct genus. Both authors placed a common tomato (*Solanum lycopersicum* L., formerly *Lycopersicon esculentum* Mill.) in subgenus *Eulycopersicon*, together with *L. pimpinellifolium* (L.) Mill. (currently *S. pimpinellifolium* L.) as coloured-fruit species. Subgenus *Eriopersicon* consisted of four (Müller, 1940) or five (Luckwill, 1943) green-fruited species. Further studies were already broadly

reviewed in literature (Grandillo et al., 2011; Peralta and Spooner, 2000; Peralta et al., 2008; Taylor, 1986). Briefly, *L. cheesmaniae* L. Riley (currently *S. cheesmaniae* (L. Riley) Fosberg) was classified together with two above-mentioned species and several new species were described. Rick (1979) placed *S. pennellii* in the genus *Lycopersicon* (*L. pennellii* (Corell) D'Arcy), within the "Esculentum complex", together with the common tomato. However, Child (1990) placed tomatoes in the genus *Solanum*, subg. *Potatoe*, sect. *Lycopersicon*. His classification was quite similar to the one currently accepted and was based on three main series: *Lycopersicon* (including *S. lycopersicum*), *Eriopersicon* and *Neolycopersicon* (including only *S. pennellii*). More recently, several new species have been described: Darwin et al. (2003) has separated *S. galapagense* from *S. cheesmaniae* populations, while Peralta et al. (2005) described *S. arcanum* and *S. huaylasense*, both previously included in *S. peruvianum*. The most recent classification of tomatoes (section *Lycopersicon*) comprises thirteen species divided into four groups: (1) *Lycopersicon* group including *S. lycopersicum*, *S. pimpinellifolium*, *S. cheesmaniae* and *S. galapagense*; (2) *Neolycopersicon* group consisting of *S. pennellii*; (3) *Eriopersicon* group

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including *S. habrochaites*, *S. huaylasense*, *S. coreneliomulleri*, *S. peruvianum* and *S. chilense*; and (4) Arcanum group represented by *S. arcanum*, *S. chmielewskii* and *S. neorickii* (Peralta et al., 2008).

Apart from studies based on plant morphology and crossing relationships, numerous studies utilizing various molecular markers were conducted in last three decades. An overview of the markers used and key results obtained are summarized in Table 1. In general, the majority of the reports supported close relationships between species placed by Child (1990) in series *Lycopersicon*. In several cases, some other species were also clustered with *S. lycopersicum*, *S. cheesmaniae* and *S. pimpinellifolium*: for example *S. chmielewskii* (Marshall et al., 2001) and *S. arcanum* (Dodsworth et al., 2016). The use of certain molecular markers, however, resulted in the classification obviously incompatible with the well-established taxonomy of tomatoes: the analysis of mitochondrial DNA (mtDNA) restriction sites placed *S. habrochaites* S. Knapp & D.M. Spooner (former *L. hirsutum* Dunal) close to *S. lycopersicum* (McClellan and Hanson, 1986). This observation was, however, not supported by other authors. Some markers allowed to separate *S. peruvianum* populations from northern and southern areas of its distribution (Peralta and Spooner, 2001; Spooner et al., 2005). Two species were then segregated from a northern *S. peruvianum* population (*S. arcanum* Peralta and *S. huaylasense* Peralta) and one from the southern population (*S. coreneliomulleri* J.F. Macbr.) (Peralta et al., 2005, 2008). This segregation was supported by the large genetic variability of *S. peruvianum* sensu lato, previously reported by several authors (Bretó et al., 1993; Miller and Tanksley, 1990).

The taxonomic position of *S. pennellii* Correll (formerly *L. pennellii* (Correll) D'Arcy) is probably the most problematic part of the classification of tomatoes. For a long time treated as a member of the genus *Solanum* with much affinity to species belonging to *Lycopersicon* genus, this almost exclusively self-incompatible

species was finally classified together with other tomato species by Rick (1979) and Child (1990). Its taxonomic position based on the molecular markers was also unclear: it was clustered together with other species, including *S. chilense* and *S. chmielewskii* (Palmer and Zamir, 1982), *S. peruvianum* and *S. chmielewskii* (McClellan and Hanson, 1986) and *S. habrochaites* (Marshall et al., 2001; Spooner et al., 2005; The 100 Tomato Genome Sequencing Consortium et al., 2014; Zuriaga et al., 2009). High distinctiveness of *S. pennellii* from other tomato taxa was also frequently suggested (Alvarez et al., 2001; Dodsworth et al., 2016; Miller and Tanksley, 1990). On the other hand, Rick (1960) reported unusually high compatibility between *S. pennellii* and *S. lycopersicum* and production of fertile interspecific hybrids. More recently it was shown that *S. pennellii* is fully crossable with all red-fruited species belonging to *Lycopersicon* series as long as they are used as a female partner (Bedinger et al., 2011). Second important feature of *S. pennellii* is its large genetic diversity, which is, in the same time, dispersed much more uniformly on the whole area of distribution when compared to *S. habrochaites* and *S. pimpinellifolium* (Rick and Tanksley, 1981). Also, *S. pennellii* displays substantial tolerance to biotic and abiotic stress. It is well-protected from some insect herbivores because of the intense biosynthesis of insecticidal glucose and sucrose esters, which are efficient against aphids (Goffreda et al., 1989, 1990) and two-spotted spider mites *Tetranychus urticae* (Lucini et al., 2015). Sugar esters were also described as potential antifungal phytochemicals (Nonomura et al., 2009). Moreover, these plants exhibit tolerance to water deficit, and sugar ester production is not affected by water availability in a longer course of time (Fobes et al., 1985). At least some accessions of *S. pennellii* are also salt-tolerant (Frery et al., 2011). All these traits make *S. pennellii* very promising secondary gene pool for breeding cultivated plants with enriched genetic basis. Moreover, some of

**Table 1**  
A summary of modern taxonomic studies on tomatoes and markers used in each study (CHES – *S. cheesmaniae*; CHIL – *S. chilense*; CHM – *S. chmielewskii*; HAB – *S. habrochaites*; LYC – *S. lycopersicum*; PEN – *S. pennellii*; PER – *S. peruvianum*<sup>a</sup>; PIM – *S. pimpinellifolium*).

No. Marker/method	Main conclusions	References
1. Chloroplast DNA (cpDNA) restriction sites	(1) Close relationship between LYC, CHES and PIM; (2) PER, CHM and CHIL combined	Palmer and Zamir (1982)
2. Mitochondrial DNA (mtDNA) restriction sites	(1) LYC and HAB clustered together; (2) PEN within PER-CHM complex	McClellan and Hanson (1986)
3. Nuclear restriction fragment length polymorphisms (RFLP)	(1) Close relationship between LYC, CHES and PIM; (2) PEN, PER and HAB separated from other taxa, with high variability	Miller and Tanksley (1990)
4. Isozymes	(1) Close relationship between LYC, CHES and PIM; (2) CHIL, PEN and PER showing high genetic variability	Bretó et al. (1993)
5. Granule-bound starch synthase (GBSSI) gene DNA sequences	(1) Close relationship between LYC, CHES and PIM; (2) Geographical separation of PER populations	Peralta and Spooner (2001)
6. Internal transcribed spacer (ITS) region of nuclear ribosomal DNA (rDNA)	(1) Close relationship between LYC, CHES, PIM and CHM; (2) PEN-HAB and CHIL-PER clusters separated	Marshall et al. (2001)
7. Nuclear DNA microsatellites	(1) Close relationship between LYC, CHES and PIM; (2) HAB and PEN highly distinct from other taxa	Alvarez et al. (2001)
8. Inter-simple sequence repeat (ISSR) polymorphisms	(1) Close relationship between LYC, CHES and PIM; (2) HAB highly distinct from other taxa	Kochieva et al. (2002a)
9. Random amplified polymorphic DNA (RAPD)	(1) Close relationship between LYC, CHES and PIM; (2) Other wild taxa including HAB in separate cluster	Kochieva et al. (2002b)
10. Amplified fragment length polymorphism (AFLP) AFLP + two nuclear gene sequences	(1) Close relationship between LYC, CHES and PIM; (2) PEN-HAB clustered together; (3) Geographical separation of PER populations	Spooner et al. (2005) Zuriaga et al. (2009)
11. Whole genome single-nucleotide polymorphisms (SNP)	(1) Close relationship between LYC, CHES and PIM; species mostly remained unresolved; (2) PEN as sister to HAB; (3) Separation of species formerly described as PER	The 100 Tomato Genome Sequencing Consortium et al. (2014)
12. Repetitive DNA data	(1) Close relationship between LYC, CHES, PIM, ARC and CHM; (2) HAB and PEN highly distinct from other taxa; (3) <i>Eriopersicon</i> group separated	Dodsworth et al. (2016)
13. Morphological data	(1) Close relationship between LYC, CHES and PIM; (2) PEN highly distinct from other taxa	Peralta and Spooner (2005)

<sup>a</sup> Described here as *S. peruvianum* complex consisting of *S. peruvianum*, *S. huaylasense*, *S. coreneliomulleri* and *S. arcanum*.

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