Tomato Fruit and its Colors

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Fruit colour represents a genetic trait with ecological and nutritional value. Plants mainly use colour to attract animals and favour seed dispersion. Thus, in many species, fruit colour coevolved with frugivories and their preferences. Environmental factors, however, represented other adaptive forces and further diversification was driven by domestication. All these factors cooperated in the evolution of tomato fruit, one of the most important in human nutrition. Tomato phylogenetic history showed two main steps in colour evolution: the change from green-chlorophyll to red-carotenoid pericarp, and the loss of the anthocyanic pigmentation. These events likely occurred with the onset of domestication. Then spontaneous mutations repeatedly occurred in carotenoid and phenylpropanoid pathways, leading to colour variants which often were propagated. Introgression breeding further enriched the panel of pigmentation patterns.

tomato colour carotenoids flavonoids lycopene naringenin chalcon anthocyanins mutations introgression breeding domestication

1. Fruit Colour and Its Evolution in Tomato Plants

Function and Evolution of Fruit Colour

Colour is one of the main qualitative attributes of fleshy fruits. Its importance is strictly dependent on its primary ecological function, which is attracting seed dispersers. In a typical example of mutualistic interaction, many plants attract animals by offering their coloured fruits as a nutritious reward in return for their seed dispersal activity. A wide range of different coloration, spanning from white to yellow, red, green, purple, and black, can stain fruit peel and flesh, according to different biotic and abiotic factors and to the developmental stage of fruits. Many fruits, especially when characterized by long ripening periods, change colour during their development, often acquiring more striking and/or contrastive hues at the end of the process.

Both the origin and the adaptive meaning of fruit colours, as well as the high variability of this trait, have been objects of study for long time. Different variables have been considered, from the role of the mutualists, to phylogenetic or environmental constraints. One of the most common interpretations is the disperser syndrome hypothesis, which is in favour of a main role of biotic factors (bird and mammal frugivories, in particular) in selecting fruit colours according to specific visual perception abilities [1]. It is quite common that seed-dispersing birds prefer red and black fruits, whereas fruits with more cryptic colours, yellow, green, or brown, are preferred by mammals frugivories [2]. Under this perspective, colour may represent a specific signal indicating precise messages, such as the degree of fruit maturity, to avoid premature fruit removal from the plant, and can facilitate recognition of specific food sources, such as certain carotenoids, as nutritional rewards [1].

Abiotic factors, mainly temperature, altitude, ripening season length, and UV-B radiation, can in turn account for part of the variation existing in nature as far as fruit colours are concerned [3]. The presence of specific classes of pigments can represent an active defence towards adverse environmental conditions or pathogens. Anthocyanins, for example, can offer photoprotection against intense solar radiation and can also absorb more solar radiation when temperature is low to increase fruit metabolic and developmental rates [1]. Thus, environmental factors can also represent drivers of diversification of fruit colour.

The most recent studies tend to adopt integrative approaches to examine the different actors in fruit colour diversification and consider dispersers and environment equally important and interacting variables [2][4]. Contrastive colours, primarily linked with anthocyanin pigments, appear in fact to be mainly associated with bird frugivories in warm areas, whereas in cold areas or where UV-B radiation is high, contrastive hues seem to be prevalent in any case, even in the presence of mammals [4]. Interestingly, the hypothesis that fruit colour may also be result of phylogenetic constraints [5][6] has progressively lost importance [7]. Colour as other fruit traits, including size and scent, can be dynamically shaped by frugivories and in many taxa, and for some groups of animals (e.g., olfactory-dependent vertebrates), are the object of coevolution more than a phylogenetic signal [8][9][10]. This could not be truer in fruits which contribute to human nutrition. The domestication process of crop plants, which have been progressively selected for adaptation to cultivation for human needs, represented an anthropogenic-driven pressure of adaptive evolution, especially in terms of fruit size, shape, colour, flavour, and texture [11][12]. However, human selection, while detecting and improving desirable phenotypic traits, largely contributed to reduce the genetic variability of cultivated plants, as occurred with tomato with the near fixation of about 25% of its genome [13]. This could have slowed down the further diversification of specific traits. In these cases, the use of wild germplasm as a source of new alleles, also known as “introgression breeding”, continues to represent an important tool to increase genetic variability in cultivated crops.

2. Carotenoid and Flavonoid Pigments as Determinants of Fruit Colour in Solanaceae

The *Solanaceae* represents one of the most important families of flowering plants, with more than 2.900 different species [14]. It includes fruit crops, such as tomato (*Solanum lycopersicum*), chili/pepper (*Capsicum* spp.), and eggplant (*Solanum melongena*), tuber vegetables, such as potato (*Solanum tuberosum*), medicinal (*Datura stramonium*, *Mandragora officinarum*, *Atropa belladonna*), and ornamental plants (*Petunia* spp., *Physalis* spp.). Some of these species represent models for the study of important physiological processes, particularly tomato and potato, tobacco (*Nicotiana tabacum*), and petunia (*Petunia x hybrida*). A great diversity of habitats and ecosystems characterize these plants, which are spread throughout the continents, with the main centre of taxonomic diversity in South America [14]. The fruits of the *Solanaceae* mostly belong to berry and capsule types and can strongly differ in size, shape, and colour [15]. Some of these traits were commonly selected in different species, particularly with domestication, whereas others appear more species-specific [11].

Colour represents a very flexible attribute, varying in *Solanaceae* from white/yellow to orange, red, purple, and brown: it mainly depends on the quantity and quality of the pigments synthesized in the fruit. These compounds belong to two different classes of secondary metabolites, carotenoids, and flavonoids, resulting from specific biosynthetic pathways, whose enzymatic steps are very conserved among the Angiosperms and well characterized in several *Solanaceae* (**Figure 1**) (for comprehensive reviews see [16][17][18][19]). While flavonoids, particularly anthocyanins, are responsible for purple, blue, and red colours, carotenoids are typical of yellow, orange, and red fruits.

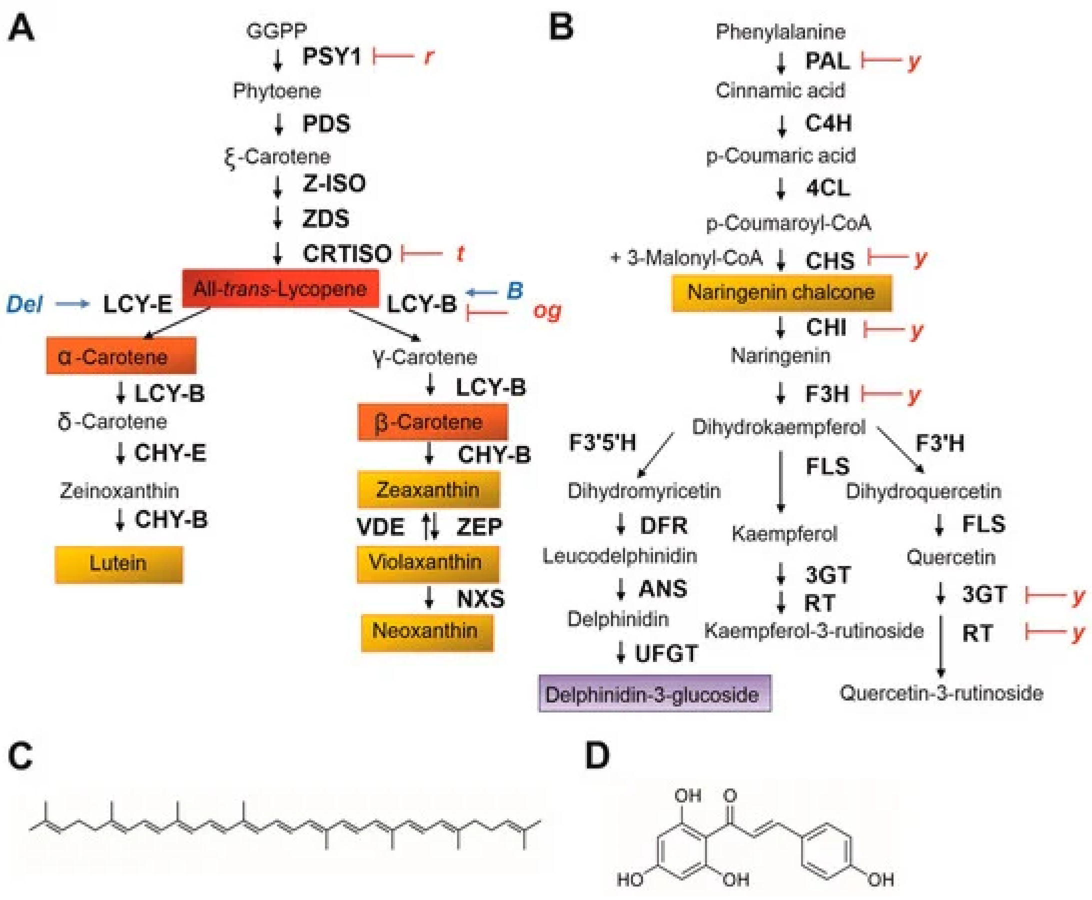

Figure 1. (**A**) The carotenoid biosynthetic pathway in tomato fruit. GGPP, geranylgeranyl diphosphate; PSY1, phytoene synthase1; PDS, phytoene desaturase; Z-ISO, ζ-carotene isomerase; ZDS, ζ-carotene desaturase; CRTISO, carotene isomerase; LCY-B, lycopene β-cyclase; LCY-E, lycopene ε-cyclase; CHY-B, β-carotene hydroxylase; CHY-E, ε-carotene hydroxylase; VDE, violaxanthin deepoxidase; ZEP, zeaxanthin epoxidase; NXS, neoxanthin synthase. The enzymatic steps inhibited (red lines) or induced (blue arrows) in the tomato mutants *r* (*yellow flesh*), *t* (*tangerine*), *Del* (*Delta*), *B* (*Beta*), and *og* (*old-gold*) are indicated. (**B**) The flavonoid biosynthetic pathway in tomato fruit. PAL, phenylalanine ammonia lyase; C4H, cinnamic acid 4-hydroxylase; 4CL, 4-coumaric acid: CoA ligase; CHS, chalcone synthase; CHI, chalcone isomerase; F3H, flavonone 3-hydroxylase; F3'H, flavonoid 3'-hydroxylase; F3'5'H, flavonoid 3'5'-hydroxylase; DFR, dihydroflavonol reductase; FLS, flavonol synthase; 3GT, flavonoid-3-O-glucosyltransferase; RT, flavonoid 3-O-glucoside-rhamnosyltransferase; ANS, anthocyanin synthase; UFGT, flavonoid 3-O-glucosyltransferase. *y* is a genetic locus associated with the mutation

in the master regulatory factor SlMYB12. Some of the steps of the flavonoid pathway downregulated in the *y* mutant are represented. (**C**) “all-*trans*-lycopene” molecular structure. (**D**) “naringenin chalcone” molecular structure.

Carotenoids are a class of terpenoid pigments deriving from the isoprenoid biosynthetic pathway, synthesized and accumulated in plastids [16]. They play different roles in plants, including photoprotection from oxidative damage in photosynthetic tissues and attraction of pollinators and seed dispersers when accumulated in chromoplasts of flowers and fruits. Flavonoids are polyphenolic compounds, synthesized through the phenylpropanoid pathway. They exhibit several biological activities in plants, including protection against different abiotic (especially UV radiation, low temperatures, low nitrogen) and biotic (herbivores and pathogens) stresses [18]. Anthocyanins are a special class of water-soluble flavonoids, generally accumulated into vacuoles, which confer colouration to several flowers and fruits.

The genetic diversification of the flavonoid pathway is mainly found at the regulatory level [18], while the evolution of the structural genes, encoding the enzymatic proteins acting along the biosynthetic way, was strongly constrained, particularly for those genes involved in the early reactions, common to multiple pathways. In this case, differences in fruit colour often rely on the presence or absence of specific classes of pigments, in turn depending on the specific activation or repression exerted by different transcription factors (TFs) on the pathway, or part of it. Three main types of factors, R2R3-MYB, bHLH, and WDR, take part in the so-called MBW ternary complexes, which are responsible for the transcriptional activation of several biosynthetic genes of the flavonoid pathway [17][20]. Different developmental and environmental factors can induce the transcription of the R2R3-MYB proteins, thus ultimately controlling the activation of the flavonoid pathway. At the same time, negative feedback loops, under control of both environmental or developmental factors, can be turned on through production of repressor proteins, such as R3-MYBs or hormonal signalling intermediates [20], to precisely fine-tune the process. Most of the phenotypes related to the flavonoid genetic diversification in fruits are caused by mutations affecting positive or negative regulators of the process, such as MYB or bHLH TFs. Contrary to flavonoids, carotenoid fruit colour mainly derives from the quantity of pigments produced or degraded, whose nature can depend on the activity of specific anabolic or catabolic genes or on their defect [17]. Both anthocyanins and carotenoids can be synthesised as photoprotective pigments as a response to high light conditions. Nevertheless, the two biosynthetic machineries are not overlapping. In many species, both flavonoids and carotenoids accumulate in fruit surface and/or flesh. In others, one of the two groups is predominant, and the other pathway can be attenuated or even switched off. However, at the genetic level, both are present, since no major losses in their regulatory or structural genes have been found in the genomes of this family of plants [11][17]. Due to their variety of anthocyanins, pepper and eggplant fruits have long been studied as suitable models for the anthocyanin pathway, whereas tomatoes, containing lower amounts of flavonoids, have been principally considered as a model for the carotenoid pathway.

In tomato, the fruit colour we can observe is a combination of different pigments accumulated in the epidermis, the sub-epidermal layer, and the fruit pericarp (flesh). Whereas in the pericarp of young fruits the green colour is predominant and due to the presence of chlorophylls, being the photosynthetic apparatus present and functional, a significant increase in the content of certain carotenoids occurs during ripening, while the thylakoid membranes in the chloroplasts break down and the plastids are converted into chromoplasts [21]. Consequently, fruit colour progressively changes from green to yellow, orange, and red, when different carotenoids and flavonoids are synthesized, and lycopene, the main carotenoid in red mature fruits, is finally accumulated (**Figure 1**A,C). The change in colour progressively occurs between the mature green stage, when all the plastids are still chloroplasts, and the fully ripe stage, when only developed chromoplasts are present [21]. This colour change is intimately interconnected with developmental signals, among which ethylene production plays a key role. Tomato is a climacteric fruit, and a production of high levels of ethylene is observed at the onset of ripening. Many of the carotenoid biosynthetic genes are regulated by this hormone [22] and thus participate in the general transcriptional regulation of the fruit ripeness, which is essentially driven by ethylene. Important mediators in this process are some TFs belonging to the MADS-box gene family [17], which, in plants, is involved in the regulation of many different developmental processes. The master regulator of the ripening cascade in tomato fruit is the *Ripening Inhibitor* (*RIN*) gene, encoding a MADS-box TF which can interact with the promoter of several genes involved in ethylene synthesis and transduction, cell wall modifications, and carotenoid biosynthesis, thus synchronising the ripeness cascade with the initiation of carotenoid production [23]. Other MADS-box TFs are involved in the regulation of the tomato fruit ripening [17], with possible influence on carotenoid production: some of them will be described in the following paragraphs.

Differently from carotenoids, mostly accumulated in tomato fruit pericarp, flavonoids (**Figure 1**B) are mainly synthesized in the single-cell layer epidermis, which is normally yellow due to the accumulation of naringenin chalcone (**Figure 1**D) from the breaker stage onward. This flavonoid likely plays an important role against fruit desiccation and offers photoprotection to the underlying photosynthetic tissues [24]. Anthocyanins are generally not present in tomato fruits, but when synthesized belong to the delphinidin-type (**Figure 1**B), and are also accumulated in the epidermis and in the sub-epidermal layer.

3. Phylogenetic Reconstruction and Human Selection of Fruit Colour in Tomato

Cultivated tomato varieties belong to the species *S. lycopersicum* var. *lycopersicum* (SLL), which originated in South America and was first domesticated in Mexico and Perú (likely in separate phases, [25]), before being introduced in Europe in the 16th century and finally, from the 19th century onwards, an object of important breeding programs in Europe and America [11]. The first described tomato fruits introduced in Europe showed some variability in colour, shape, and size, and yellow and red were described as two possible colours [26]. SLL belongs to the so-called “tomato clade”, a group of thirteen Solanum relative species, further divided in four subgroups [27][28] (**Figure 2**A). SLL is included in the section Lycopersicon, a restricted group of tomato close species, all self-compatible, to which *Solanum pimpinellifolium* (SP) also belongs, considered the closest relative of SLL, which produces red fruits (**Figure 2**A). Red fruits are also produced by the var. *cerasiforme* of *S. lycopersicum* (SLC), regarded as an intermediate between SP and SLL and the direct ancestor of the cultivated varieties due to its close genetic relationship with them [13][25]. *Solanum galapagense* and *Solanum cheesmaniae* are both endemic to the Galapagos Islands, and produce small orange-yellowish fruits [29][30]. They also belong to the section Lycopersicon (**Figure 2**A). In this subgroup of the tomato clade, red and orange carotenoids represent the main fruit pigments.

The orange colour shown by the Galapagos Islands species, later introgressed in SLL, is due to a high accumulation of β-carotene, de-novo produced from *trans*-lycopene thanks to a high expression of the dominant *BETA* (*B*) allele of a chromoplast specific *lycopene β-cyclase* (*LCY-B*) gene, which in wild type tomato is generally poorly transcribed [31][32] (**Figure 1**A). On the contrary, the *old-gold* (*og*) recessive allele of *LCY-B* induces higher levels of *trans*-lycopene production and leads to dark red fruits [31] (**Figure 1**A). Other two different “orange” alleles identified in SLL are the *Delta* (*Del*) dominant allele, introgressed from the wild species *Solanum pennellii*, which induces increased expression of the *lycopene δ-cyclase* (*LCY-E*), resulting in increased transformation of lycopene in δ-carotene [31][32], and the *tangerine* (*t*) allele, a mutated allele of the *carotene isomerase* (*CRTISO*) gene, which leads to the main accumulation of *cys*-lycopene and other carotenoids, at the expense of the red *trans*-lycopene [32][33][34] (**Figure 1**A). Yellow-coloured tomato fruits are due to recessive alleles of the *yellow flesh* (*r*) locus, which correspond to mutations in the *phytoene synthase 1* (*PSY1*) gene, encoding the first committed enzyme in the carotenoid biosynthetic pathway [32][35] (**Figure 1**A). In this case, the yellow colour is due to the flavonols present in the fruit peel and to other carotenoids, such as lutein, which are normally present in green tissues. The brown colour of some tomato fruits, exhibited especially by some heirloom tomatoes, is instead dependent on the superimposition of the red lycopene colouration with the green colour of the chlorophylls, which, usually degraded during tomato ripening, are here retained because of the inhibition of their degradation.

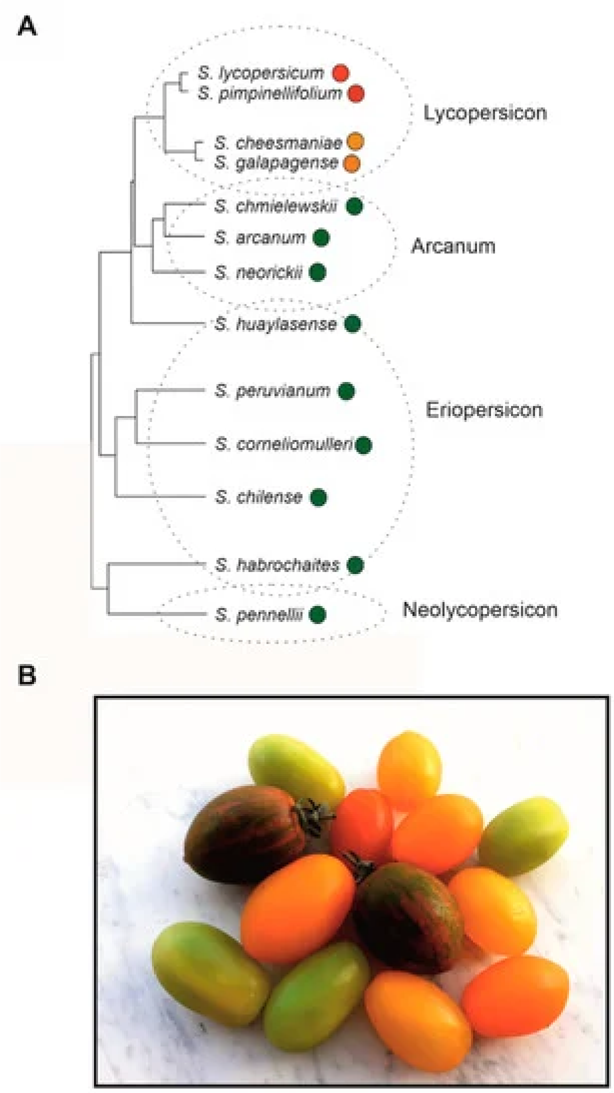

Figure 2. (**A**) Phylogenetic tree of Solanum species belonging to the tomato clade, divided in the four subgroups identified by [27][28]. Redrawn with simplifications from [29], with the addition of the fruit colour, represented by coloured circles close to the species names. (**B**) Photo of a group of ripe *Solanum lycopersicum* fruits exhibiting possible colour variants in the carotenoid/chlorophyll pathway: red, orange, yellow, green, and “green stripe”-like colourations are shown.

The phenotype is called *green flesh* (*gf*) and is due to different types of mutations identified in a tomato homolog of the *staygreen* (*SGR*) gene of rice, which encodes a chloroplast protein regulating the degradation of chlorophyll during senescence [36][37]. All these different genotypes thus originated a wide panel of different carotenoid colourations of tomato fruits (**Figure 2**B). Other peculiar tomato fruit colours originate from variants in the flavonoid pathway, such as the pink colour associated with the locus *y*: this is caused by a mutation in the master regulatory factor SlMYB12, with the downregulation of the expression of several structural genes of the flavonoid pathway and the absence of the yellow-coloured flavonoid naringenin chalcone in the fruit peel, which remains transparent [13][38]. By combining the loci *y* and *r* in the same genotype an almost white tomato fruit can be produced, characterized by a very pale-yellow flesh [11]. When the *SGR* gene is also mutated in a *y* x *r* background, tomato fruits remain green, since they do not contain carotenoids and flavonoids and cannot degrade chlorophylls during ripening [39].

Naringenin chalcone (**Figure 1**D) represents the main flavonoid synthesized in tomato fruits, together with lower amounts of the flavonols quercetin-3-rutinoside (rutin) and kaempferol-3-rutinoside (**Figure 1**B). Other trace glycosides of naringenin chalcone, quercetin, and kaempferol have been identified [38], but the phenylpropanoid biosynthetic pathway is blocked downstream and does not allow the production of other important classes of polyphenols, including anthocyanins. Nevertheless, wild related Solanum species can produce anthocyanins in their fruit peel (**Figure 3**A), and this trait was repeatedly introgressed into SLL through interspecific crosses [40]. One of the most studied anthocyanin-enriched phenotypes was *Anthocyanin fruit* (*Aft*), derived from interspecific cross with *Solanum chilense* [40][41][42] (**Figure 3**B). A similar phenotype, named *Aubergine* (*Abg*) [42], was introgressed from *Solanum lycopersicoides*. An even more marked anthocyanin pigmentation was obtained in the *Aft* or *Abg* tomato lines with the inclusion of the *atroviolacea* (*atv*) locus, introgressed from *S. cheesmaniae* [40][42] (**Figure 3**B,C). All these anthocyanin phenotypes are controlled by genes inherited from wild Solanum species, whose fruits in nature are commonly green, but are also able to accumulate purple anthocyanins in specific environmental conditions [30] (**Figure 3**A). Excluding the restricted group of Solanum closest relatives above described, the green fruit phenotype is found in all the other subgroups of the tomato clade, from *Solanum chmielewskii* to *S. pennellii* (**Figure 2**A). These are all species characteristic of the Andean regions of South America and the geographic distribution, particularly the altitude of their typical habitats, may explain the ability they developed and maintained to produce, when necessary, secondary metabolites allowing photoprotection and/or protection of the fruit from low temperatures.

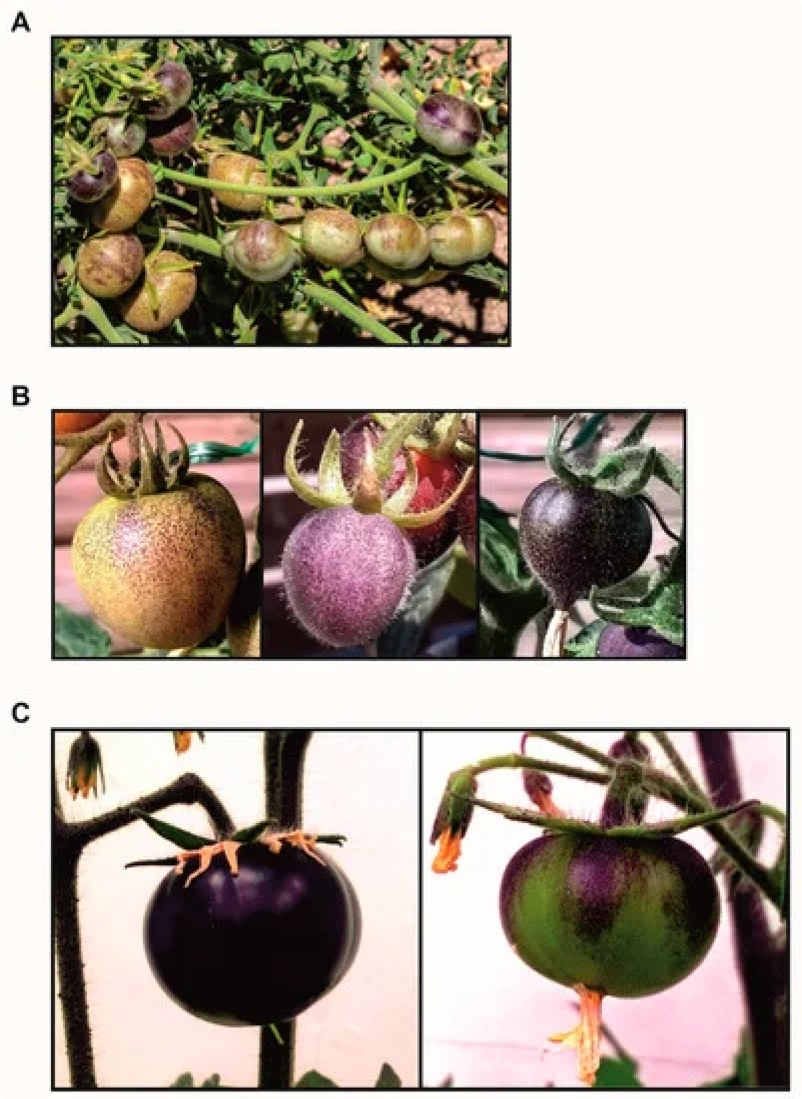

Figure 3. (**A**) Photo of *Solanum chilense* anthocyanin-spotted green ripe fruits from plants spontaneously grown in Chile, Toconao, Quebrada de Jere (−23.14553°, −067.98998°, 2703 m, 12 dec 2012) (kindly provided by Mr. M. Giorgetta). (**B**) SLL fruits, cv. MicroTom, showing different levels of anthocyanin pigmentation at the mature green stage of ripening. From left to right: *Aft*/*Aft* x *ATV*/*atv*, *Aft*/*Aft* x *atv*/*atv*, and *Aft*/*Aft* x *atv*/*atv x hp2*/*hp2* genotypes. (**C**) SLL fruits, cv. Ailsa Craig, at mature green with *Aft*/*Aft* x *atv*/*atv* genotype, and complete or partial anthocyanin pigmentations.

In addition to genes involved in carotenoid and flavonoid synthesis and in chlorophyll degradation, other genes have been shown to influence tomato fruit colour. Mutations in negative regulators of the upstream light-signalling pathways which regulate both carotenoid and flavonoid biosynthesis, such as the *high pigment* (*hp*) mutations [43][44], increase the amount of all the pigments normally produced under light stimulation (carotenoids, flavonoids, and chlorophylls). *hp* tomatoes thus show a darker colour of both peel and flesh. Other regulators of fruit colour are some TFs involved in fruit ripening: besides the already mentioned MADS-box TF RIN [23][45], it is worth to remember the SBP-box TF Colourless Non-Ripening (CNR) [46], and the NAC TF Non-Ripening (NOR) [47], as well as some components of the ethylene signalling pathway, such as Never Ripe (NR) [48] and Ethylene Insensitive2 (EIN2) [49][50][51].

Going backwards in the phylogeny of SLL, it appears that the red colour, typical of the fruits produced by SP, likely represented the original colour of the first domesticated tomato plants and it is still the most typical of the modern varieties (**Figure 2**A). Red colour is also shown by the fruits of the several cultivated landraces of SLC, which in South America still experience occasional gene flows with the wild relative SP [13][52]. Spontaneous mutations in the carotenoid pathways may have occurred on several occasions during tomato cultivation and some of them, such as the *yellow flesh*, even in the original areas of tomato domestication, since this colour was already present in some tomato genotypes described in Europe in the 16th century [53]. Other colours, such as the orange or brown, which are typical of heirloom accessions worldwide spread, may have appeared in similar ways.

Genomic analyses into the history of tomato domestication identified the principal traits under selection in fruit size and taste: fruit mass, in particular, was the key character selected by men [13]. However, studying tomato domestication and breeding, structural variants also affecting the expression of genes involved in lycopene metabolism were recently detected. They would indicate reduction of lycopene from SP to SLC and subsequent settlement in both the heirloom and modern populations of the big-fruited SLL tomato, suggesting that the trait could have been under selection during domestication but not in the more recent phases of tomato improvement and modern breeding [54]. A reduction in the level of β-carotene was also highlighted in the transition of SP to SLC in the South American areas of domestication, together with tendencies toward larger fruit size, thicker pericarps, higher number of locules, lower content of citric acid, and of soluble solids, all considered typical traits of tomato domestication syndrome [25].

The green colour of fruits (**Figure 2**A), together with allogamy and self-incompatibility, thus represents a primitive trait in the tomato clade [27]. A recent study identified functional PSY1 enzyme, with similar catalytic activity, in both green-fruited and red-fruited Solanum species [55]. Therefore, it seems that a major difference in *PSY1* expression, probably due to important changes in *PSY1* promoter/5′-UTR regions, with the loss of regulatory elements involved in abiotic stress response and the acquisition of new ethylene-responsive elements, was important in the association of carotenogenesis with ripening, thus contributing to pericarp colour variation from green to red during tomato domestication [55]. Concomitantly with this, red-fruited tomato species lost the ability to synthesize anthocyanins, possibly because of differential climatic adaptations or the same domestication process.

In addition to the effects of spontaneous mutations, diversity in fruit colour existing in SLL varieties may be ascribed to new alleles introgressed from wild tomato genomes into modern cultivars. Changes in fruit colours may have also occurred as a secondary consequence of breeding strategies aimed at improving other traits. More recently, thanks to the increasing awareness of the beneficial effects on human health of certain classes of secondary metabolites, colour has become a major determinant of the economic value of tomato: therefore, enrichment of its fruits with specific groups of pigments, such as anthocyanins and other flavonoids, has become a novel goal of genetic engineering or breeding. These approaches led to the production of high-flavonol [56] and high-anthocyanin [40] tomatoes (**Figure 3**C), further increasing the variability of the tomato surface pigmentation.

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