HAL
open science

Phenotypic diversity in wild and cultivated melons (Cucumis melo)

Michel Pitrat

To cite this version:

Michel Pitrat. Phenotypic diversity in wild and cultivated melons (Cucumis melo). Plant Biotechnology, 2013, 30 (3), pp.273 - 278. 10.5511/plantbiotechnology.13.0813a . hal-02648270

HAL Id: hal-02648270

https://hal.inrae.fr/hal-02648270

Submitted on 29 May 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Plant Biotechnology 30, 273–278 (2013)
DOI: 10.5511/plantbiotechnology.13.0813a

Review

Phenotypic diversity in wild and cultivated melons (*Cucumis melo*)

Michel Pitrat

INRA, UR1052, Génétique et amélioration des fruits et légumes, CS 60094, 84143 Montfavet cedex, France
* E-mail: Michel.Pitrat@avignon.inra.fr Tel: +33-4-32-72-27-17 Fax: +33-4-32-72-27-02

Received June 14, 2013; accepted August 13, 2013 (Edited by H. Ezura)

Abstract Like many crops, cultivated melons present a very large phenotypic polymorphism compared with the low phenotypic polymorphism of wild melons. Domestication has not been intensively studied and the genetic control of domestication traits is still poorly understood. The results of the subsequent diversification and selection processes are the present day types of melons. Genetic control of a majority of the diversification traits is under recessive genetic control: sex expression, fruit shape, sutures, number of placentas, gelatinous sheath around the seeds, white flesh colour and so on. Other phenotypic traits are dominant (orange flesh colour, netting, yellow colour of mature fruit in the Amarillo type and so on) as are most of the disease resistances. Presence of the same traits in very different botanical groups can be the result of parallel evolution but also of intercrossing between groups and selection of preferred alleles. New results (genome sequencing) and methods will allow a better understanding of the genetic control of domestication and diversification.

Key words: Diversification, domestication, genetic control, genetic resources.

Plant domestication represents "a continuum of increasing codependence between plants and people.… Domesticated plants cannot reproduce or survive without the investment of a large amount of human labour" (Gross and Olsen 2010). In this paper, the word "wild" is used in opposition to "domesticated", meaning that wild plants can grow and reproduce without the help of man. The term "feral" refers to populations which return from a domesticated to a wild status. Man is dependent from domesticated plants for his food and domesticated plants are dependent from men because they cannot survive in competition with weeds without agriculture. The "domestication syndrome" has been studied mainly in cereals and corresponds to seed dormancy, fragile or tough rachis (shattering), plant structure, inflorescence structure… (Hammer 1984). In the case of vegetables, it corresponds mainly to larger fruit, leaf or root size and in some cases to changes in the reproduction mode; for instance wild tomatoes are characterized by very small fruits (1–2 g) and a tendency towards allogamy with style exertion. The wild populations observed today cannot be considered as the ancestors of our modern cultivars. These populations correspond to evolution under natural selection while cultivars correspond to evolution under man-driven or artificial selection, both from common ancestors.

Diversification is a second step after domestication and has produced the cultivars, cultigroups and botanical varieties. Diversification is particularly spectacular in some vegetables like *Brassica oleracea* (cabbage, cauliflower, kohlrabi, broccoli, Brussels sprouts…), *Brassica rapa* (Chinese cabbage and turnip), *Beta vulgaris* (beet root and Swiss chard but also sugar beet) or *Apium graveolens* (leaf or root). As mentioned above, domestication is a continuum and the limit between domestication and diversification is not clear cut. Moreover two or several independent domestication events may have taken place at different time or in different places.

Melon (*Cucumis melo* L.) is an old world plant and was probably cultivated more than 2000 years BCE (Andrews 1956; Decker-Walters 1999; Keng 1974; Manniche 1989; Meirano 2000; Moldenke and Moldenke 1952; Schoske et al. 1992; Stol 1987; Vishnu-Mittre 1974; Walters 1989). Wild melons (i.e. not cultivated) can be found in Africa and Asia and a large diversity of cultivars is grown on all continents.

This review focuses on the genetic control of some traits involved in domestication or diversification of melon.

What are wild melons?

Typical wild melons, sometimes called "weedy melons", can be observed in Africa and Asia. They are characterized by small leaves and flowers, stems with

This article can be found at http://www.jspcmb.jp/
Published online September 27, 2013

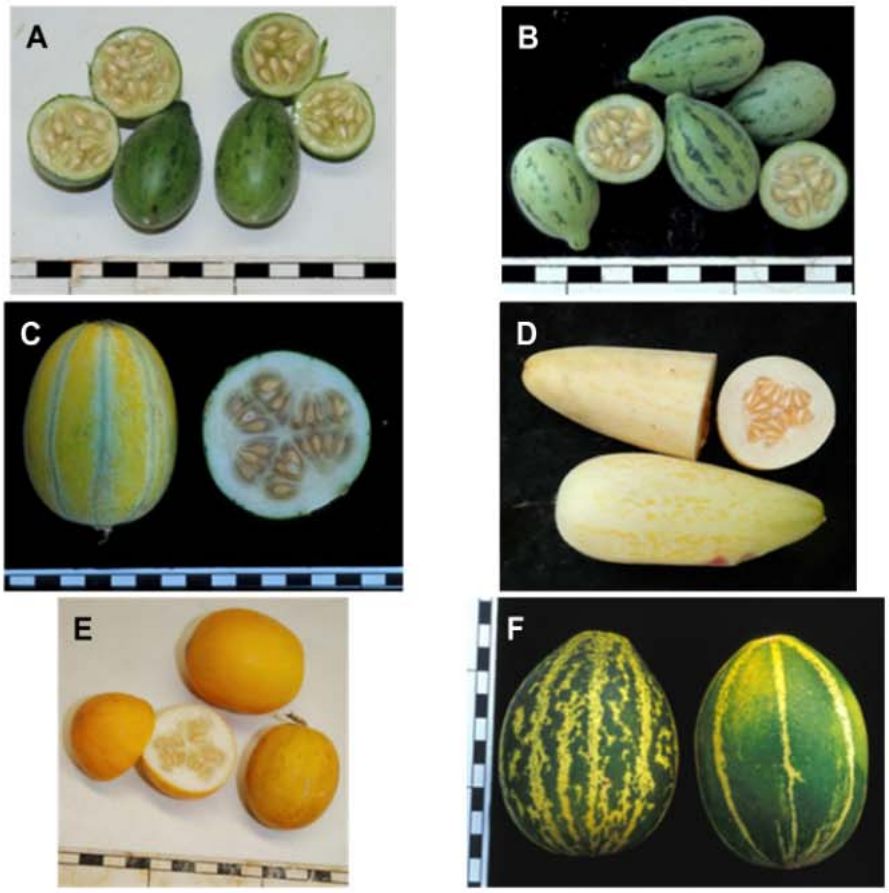

Figure 1. Fruits of typical wild melons (A and B), of wild melons growing close to cultivated types and with intermediate type (C=presence of sutures, D=larger size), of the *chito* group which could represent a feral type (E) and of a primitive cultivated type (F=*tibish* group).

a small diameter and numerous ramifications. They are monoecious. The fruits are oval shaped, sometimes round, small (20 to 50 g) and smooth: neither netted nor ribbed or wrinkled (Figure 1A, B). The fruit epidermis is usually light green with dark green dots or stripes, without sutures. The flesh is light green, very thin. There are three placentas and no cavity between the placentas. The seeds are small and embedded in a gelatinous sheath. Maturation can be climacteric or non-climacteric with or without peduncle dehiscence.

The wild species *Cucumis pubescens*, *C. trigonus*, or *C. turbinatus* are now considered as synonyms of *C. melo*. The status of *C. picrocarpus* recently described as the most closely related species of *C. melo* (Sebastian et al. 2010) is not very clear, as no data on the sexual compatibility with melon are available.

In Central America and the Caribbean Islands, the *chito* group (Naudin 1859) could represent feral melons. It is not cultivated. The fruits are small, round with a yellow skin (Figure 1E). The flesh is thin, light green. The seeds are small with a gelatinous sheath. Except for the yellow skin colour, they look like the "wild" melons described above. The New World is not the centre of origin of melon and this type corresponds to a return to a wild status from cultivated melons.

Two sub-species have been described: subsp. *melo* is characterized by long and spreading hairs on the ovary or the young fruit, subsp. *agrestis* by short and appressed hairs (Kirkbride 1993). The word "agrestis" had first been used to describe the tribe of "wild" melons (Naudin 1859). A lot of confusion has resulted from these two meanings as the wild or weedy melons ("agrestis" *sensu* Naudin and briefly described in the above paragraph) belong to the subsp *agrestis sensu* Kirkbride with short hairs or to the subsp *melo* with long hairs on the ovary and the young fruit. Many cultivated melons, for instance the *acidulus*, *momordica*, *conomon* or *makuwa* groups, belong to the subsp. *agrestis sensu* Kirkbride.

Domestication traits

It is expected that domestication traits are present in almost all cultivars and absent in wild accessions. On the opposite, diversification traits are present in only some cultivars or cultigroups but not in all of them. For instance, orange flesh colour or andromonoecy are diversification traits and not domestication traits as many cultivars have green flesh or are monoecious like wild

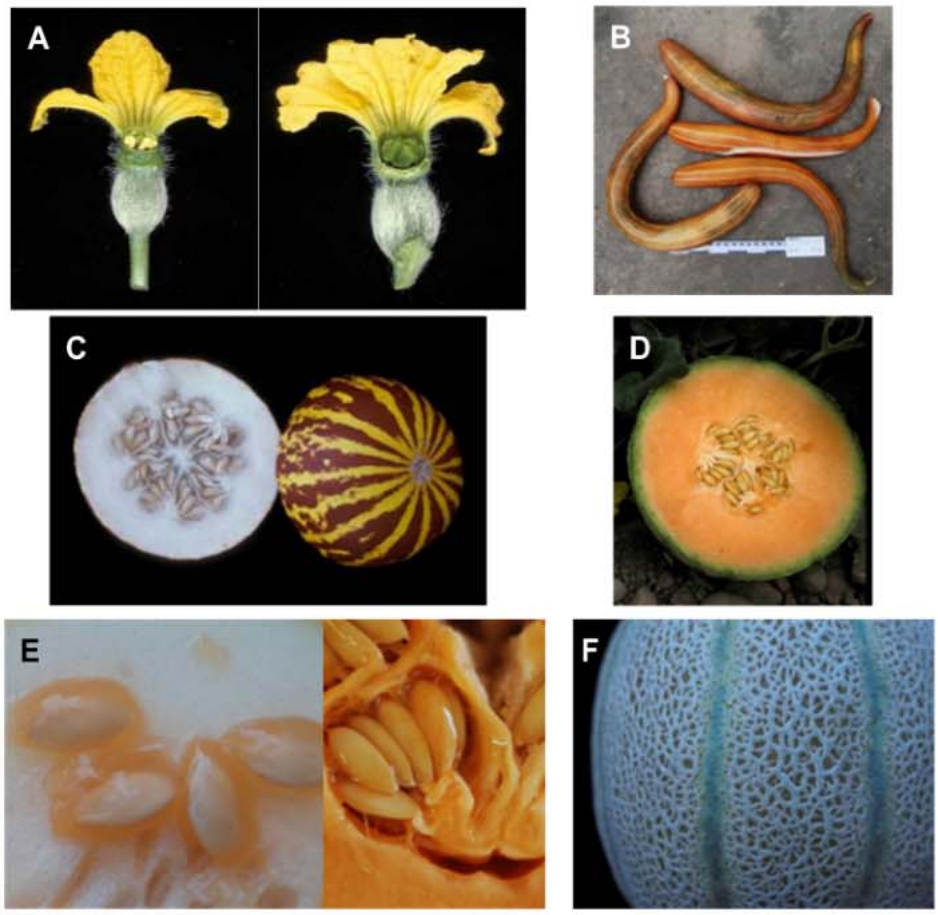

Figure 2. Some diversification traits in cultivated melons. A: Perfect flower (left) and female flower (right). B: Fruit shape, size and exocarp colour (*flexuosus* group). C: exocarp colour and five placentas (*dudaim* group). D: Orange flesh colour (*cantalupensis* group). E: Presence (left) or absence (right) of a gelatinous sheath around the seeds. F: Netted exocarp and presence of sutures (*reticulatus* group).

melons.

Domestication traits have been studied in cereals with the shattering of rice or wheat, the inflorescence structure of maize or the plant structure of rice or maize. Seed dormancy is also a domestication character found in many species. Indeed a negative selection has been applied by farmers because they want that all the seeds germinate at the same time and not for several years in one field after sowing. In the case of melon, seed dormancy has not been clearly described but it is commonly observed in seed banks that the wild accessions have erratic germination rate.

All cultivated melons have larger fruits, non-bitter and thicker flesh, larger seeds and larger leaves than the wild melons. These characters can be considered as domestication traits. Many cultivated melons have cucurbitacins responsible for bitterness in the leaves or the roots (for instance the *makuwa*, *chinensis* or *cantalupensis* groups) but no cultivated melons have bitter fruits. Absence of cucurbitacins in mature fruits can also be considered as a domestication trait.

All the other characters like sex expression, fruit shape, exocarp and flesh colour, sugar content, aroma… should be considered as diversification or selection traits.

In Africa or Asia, wild melons can grow close to cultivated fields and cross pollination can occur. Some intermediate or recombinant phenotypes between typical wild and cultivated melons can be observed with larger fruits (100–200 g), light orange flesh, with sutures on the fruits or andromonoecious (Figure 1C, D). Nevertheless, despite gene flow corresponding to back-crosses, the wild melons remain quite typical.

The most typical trait of domestication i.e. the loss of fitness or competitiveness towards weeds without agricultural practices has not been analysed in any plants and is poorly understood.

Diversification traits and their genetic control

Modern cultivars exhibit a large phenotypic diversity, mainly for fruit traits. This diversity is the result of positive or negative selection by farmers during millennia. Many mutations with "negative" effect which are now maintained in gene banks have not been selected by farmers and are not present in heirloom or traditional

cultivars: chlorophyll deficiency, male-sterility, nectarless….

Many traits have a Mendelian inheritance and F_1, F_2 and back-cross progenies are sufficient to study their genetic control. For quantitative traits such as sugar content, disease resistance, fruit shape and weight, earliness… homozygous "immortalized" genotypes such as doubled haploid lines, recombinant inbred lines or introgression lines are very powerful tools. The name and the symbol of the genes in the following sections of this paper are according to the last gene list for melon published by Cucurbit Genetics Cooperative (Dogimont 2010–2011).

Sex expression

Wild melons are monoecious (Figure 2A). A majority of cultivars is andromonoecious and a few accessions from China are hermaphrodite. Some wild melons growing close to cultivated melons can be andromonoecious (Fujishita 1983). Two recessive genes have been described: at the locus *a*, the recessive allele *a* controls the presence of stamens in female flowers and the allele a^+ controls the absence of stamens in female flowers; at the locus *g*, the recessive allele *g* controls the presence of one type of flowers on the plant and the allele g^+ controls two types of flowers on one plant. The combination of these alleles lead to four phenotypes: monoecious [a^+g^+] corresponding to the wild melons, andromonoecious [ag^+], gynoecious [a^+g] and hermaphrodite [ag]. Recently a dominant control of andromonoecy has been described in the *tibish* group (Abdelmohsin et al. 2012).

Fruit size and shape

Wild melons have small (20–50 g) round or oval fruits. In cultivars, the fruit shape can vary from flat to very long (up to 1.8 m) in the *flexuosus* group (Figure 2B). Fruit weight is commonly between 1 and 2 kg but smaller (200–300 g) or larger (more than 5 kg) fruits can be observed. The pleiotropic effect of the presence or absence of stamens in the female flowers (locus *a*) on the fruit shape must be mentioned: monoecious plants have usually larger and more elongated fruits than quasi-isogenic andromonoecious plants. Fruit and ovary shape are correlated and QTLs mainly recessive for fruit and ovary length and width have been described. Fruit weight is also under polygenic mainly recessive control.

Fruit exocarp

The fruits of wild melons are smooth, typically light green with dark green spots, sometimes uniform light green colour. The primary and secondary fruit colours of cultivars can be white, bright yellow, brown, orange, light green or dark green. The pattern can be uniform (honeydew, Amarillo), with dots (Piel de sapo) or stripes (*dudaim* Figure 2C). The exocarp can be netted (*reticulatus*) or wrinkled (Tendral, Yuva). Sutures can be present (Charentais, Ogen) or not (Figure 2F). Several genes involved in the control of these traits are recessive: presence of sutures (allele *s*), uniform colour (alleles Mt^+, *spk*, *st*), white colour of mature fruit (allele *w*). Other genes are dominant: yellow colour of mature fruit (allele *Y*), netted fruit exocarp (Figure 2F).

Fruit flesh and seeds

Fruits of wild melons have a very thin light green flesh, which is not sweet, sometimes bitter, without aroma. They have three placentas and the small seeds are embedded in a gelatinous sheath. The flesh of cultivated melons can be green like the wild types (presence of chlorophyll), white (one recessive allele *wf*) or orange (presence of β-carotene, dominant allele gf^+) (Figure 2D). Melon can be sweet (*cantalupensis*, *reticulatus*, *inodorus*, *ameri*… groups) or not (*acidulus*, *flexuosus*, *conomon*, *tibish*… groups). One main recessive gene (allele *suc*) and recessive QTLs are involved in the genetic control of sugar accumulation. Low acidity or high pH is also controlled by one recessive gene (allele pH^+). Although three placentas is the most common phenotype in cultivated melons, some types (*dudaim*, *conomon*, *chinensis*, *tibish* groups) are characterized by five placentas (allele *p*). The absence of a gelatinous sheath around the seeds (*cantalupensis*, *ameri*, *inodorus*… groups) is under a monogenic recessive control (allele Gs^+) (Figure 2E). Seed colour can be white (allele *Wt*) or brown (pleiotropic effect of *red stem* allele).

Absence of cucurbitacins responsible for bitterness in the plant and/or the fruit is controlled by recessive alleles at several loci (Bi^+, $Bif\text{-}1^+$, $Bif\text{-}2^+$, $Bif\text{-}3^+$).

For other traits the genetic control has not been published: flesh texture varies from mealy (*momordica* group) to firm and crispy (*acidulus* group) to juicy (*ameri* group); volatile compounds are present (*dudaim*, *cantalupensis*…) or absent (*acidulus*, *conomon*…); seed size varies between 10–12 seeds per gram to 290–300 seeds per gram.

Fruit maturation

Maturation of wild melon can be climacteric or non climacteric, with or without fruit peduncle dehiscence. Dominant major genes (*abscission layer*) and QTLs (*eth*) are involved in the genetic control of climacteric crisis.

Disease and pest resistance

Wild accessions are usually susceptible to the viruses, bacteria, fungi, insects or nematodes that attack melons. However some resistant wild accessions have been identified: PI 180280 and PI 180283 resistant to *Papaya ringspot virus* (PRSV), PI 140471 to *Didymella bryoniae*, PI 536473 to *Acidovorax avenae* subsp. *citrulli*.

In contrast, in some cultigroups (*momordica* and

acidulus from India, *conomon* and *makuwa* from Far-East) many resistances have been described. Some resistance are under recessive genetic control: *Melon necrotic spot virus* (MNSV, allele *nsv*), *Cucumber vein yellowing virus* (CVYV, allele *cvy-2*), *Cucurbit aphid borne yellows virus* (alleles *cab-1* and *cab-2*), *D. bryoniae* (allele *gsb-5*), to powdery mildew *Podosphaera xanthii* (in accession 90625), *Cucumber mosaic virus* (CMV, QTLs), *Fusarium oxysporum* f.sp. *melonis* race 1.2 (QTLs), *Pseudoperonospora cubensis* (QTLs).

Many pest and disease resistance are also under dominant genetic control: *F. oxysporum* f.sp. *melonis* races 1 or 2 (alleles *Fom-1* and *Fom-2*), *Aphis gossypii* (allele *Vat*), powdery mildew (several loci and alleles), *Alternaria cucumerina* (allele *Ac*), *D. bryoniae* (several loci), *P. cubensis* (several loci), PRSV (locus *Prv*), *Zucchini yellow mosaic virus* (ZYMV, allele *Zym*), CVYV (locus *Cvy-1*), *Cucurbit yellow stunting disorder virus* (allele *Cys*), MNSV (alleles *Mnr-1* and *Mnr-2*), leafminer *Liriomyza trifolii* (allele *Lt*)….

Parallel evolution

Convergent evolution may be defined as the selection of the same phenotypic traits in independent lineages, for instance in related species: andromonoecy has been selected in melon, but also in watermelon (*Citrullus lanatus*) and cucumber (*Cucumis sativus*). Parallel evolution is the selection of the same phenotypic trait in sexually compatible populations.

Many phenotypic traits listed above are present in both sub-species and in different cultigroups. For instance andromonoecy has been selected in the sub-species *melo* (*cantalupensis*, *reticulatus*, *dudaim* groups) and in the sub-species *agrestis* (*conomon*, *makuwa*, *tibish* groups) [Note: I have made mistakes in previous publications (Pitrat 2008) including the *tibish* group in the subsp *melo*; it belongs to the subsp. *agrestis* (Figure 1F)]. Similarly, resistance to *F. oxysporum* f.sp. *melonis* races 1 and 2 (alleles *Fom-1* and *Fom-2*) or to MNSV (allele *nsv*), presence of sutures, bright yellow epicarp, sugar accumulation... are also present in both sub-species. Other traits have been identified only in some cultigroups, for instance CMV or *P. cubensis* resistance. Different hypothesis can be formulated:

- The mutation(s) occurred before domestication(s), but in this case the trait should be observed in some present-day wild melon accessions;
- The mutations(s) occurred one time and was spread in the cultivated populations belonging to different sub-species and cultigroups by cross-pollination and selection;
- The mutation(s) occurred several times independently in the different cultigroups.

There are no archaeological data to support one of these hypotheses for each phenotypic trait. The molecular data on the allelic diversity of phenotypic traits are still scarce. For monoecy/andromonoecy, the locus *a* codes for an ACC synthase gene (*CmACS7*); the functional *CmACS7* allele corresponds to the monoecy phenotype and the non-functional allele to the andromonoecy phenotype. Among 41 monoecious accessions, 11 haplotypes were identified and among 65 andromonoecious accessions, only one haplotype was identified (Boualem et al. 2008). Similarly the same point mutation has been identified in the gene *nsv* for MNSV resistance in accessions from different geographical origins and belonging to different sub-species and cultigroups. In both cases it seems that the mutations conferring the new phenotypes (andromonoecy or resistance to MNSV) occurred only one time and quite recently.

Conclusions

The genetic control of phenotypic traits typical of melon domestication is still poorly understood. Fruit size and absence of bitterness in the fruit can be considered clearly as domestication traits. Most of the genes and QTLs involved in diversification or selection traits are recessive (including absence of bitterness which could be a domestication trait), except disease resistance. Recessive genetic control corresponds often to non-functional proteins due to point mutation, stop codon, transposon insertion… but does not mean a loss of a phenotypic trait. The decrease of ethylene concentration in the flower buds due to the non-functional *CmACS7* allele leads to the appearance of stamens. Similarly decreases of hormone levels in the fruits can result in larger fruits due to an increase of cell numbers or cell sizes.

Many pest and disease resistances which are under dominant genetic control have been identified in accessions from India in the *momordica* and *acidulus* groups such as powdery mildew, Fusarium wilt, *A. cucumerina*, *A. gossypii*, ZYMV, PRSV, CVYV… Recessive genetic control is found for CMV, Fusarium wilt race 1.2 or MNSV in Far-Eastern accessions. Vavilov speculates that dominant alleles are mainly found in the centre of origin and recessive alleles in the periphery (Vavilov 1957).

If we look at the number of diversification traits between wild melons and the different cultigroups, the *tibish* group can be considered as the most primitive. Indeed it differs from the wild melon only by the "five placentas", the "andromonoecious" and the slightly larger fruits characters.

How many domestication events have occurred? Two sub-species have been described (*melo* and *agrestis*) and wild melons are observed in these two sub-species. The

sub-species *agrestis* is found mainly in Asia from India to Far-East with the *momordica*, *acidulus*, *conomon*, *makuwa*, *chinensis* groups but also in Africa with the *tibish* group and in Central America with the *chito* group. The sub-species *melo* is found in India, Central and Western Asia, Africa, Europe and America with the *cantalupensis*, *reticulatus*, *inodorus*, *chandalak*, *ameri*, *flexuosus*, *chate* or *dudaim* groups. Data from neutral nuclear (RAPDs, SSRs…) and chloroplastic (SNPs, SSRs) genome diversity suggest a polyphyletic origin of melon with two or three domestication events (Serres-Giardi and Dogimont 2012; Tanaka et al. 2013): one leading to the sub-species *agrestis* in India or Eastern Asia, another one leading to the subspecies *melo* in Africa or Western Asia and a third one in Africa for the *tibish* group also belonging to the sub-species *agrestis*. The absolute and relative time of these domestications events is unknown. The case of the *chito* group has already been discussed above and could represent feral melons.

In the future, the availability of the sequence of the melon genome (Garcia-Mas et al. 2012) with eco-TILLING or resequencing methods will allow to have a better understanding of the evolution of melon by studying the allelic diversity of genes and QTLs controlling phenotypic traits involved in domestication or diversification.

References

Abdelmohsin ME, ElJack AE, Yousif MT, Ahmed EA, Pitrat M (2012) Inheritance of andromonoecy in Tibish. In: Sari N, Solmaz I, Aras V (eds) *Cucurbitaceae 2012. Proceedings of the Xth EUCARPIA Meeting on Genetics and Breeding of Cucurbitaceae*, Antalya (TR), 15–18/10/2012. Çukurova University, pp 427–431

Andrews AC (1956) Melons and watermelons in the classical era. *Osiris* 12: 368–375

Boualem A, Fergany M, Fernandez R, Troadec C, Martin A, Morin H, Sari M-A, Collin F, Flowers JM, Pitrat M, et al. (2008) A conserved mutation in an ethylene biosynthesis enzyme leads to andromonoecy in melons. *Science* 321: 836–838

Decker-Walters DS (1999) Cucurbits, sanskrit, and the Indo-Aryas. *Econ Bot* 53: 98–112

Dogimont C (2010–2011) Gene list 2011 for melon. *Cucurbit Gen Coop Rep* 33–34: 104–133

Fujishita N (1983) Genetic diversity and phylogenetic differentiation in melon. *Cur Topics Plant Breed* 24: 3–21

Garcia-Mas J, Benjak A, Sanseverino W, Bourgeois M, Mir G, González VM, Hénaff E, Câmara F, Cozzuto L, Lowy E, et al. (2012) The genome of melon (*Cucumis melo* L.). *Proc Natl Acad Sci USA* 109: 11872–11877

Gross BL, Olsen KM (2010) Genetic perspectives on crop domestication. *Trends Plant Sci* 15: 529–537

Hammer K (1984) Das Domestikationssyndrom. *Kulturpflanze* 32: 11–34

Keng H (1974) Economic plants of ancient north China as mentioned in *Shih ching* (Book of Poetry). *Econ Bot* 28: 391–410

Kirkbride JH (1993) Biosystematic Monograph of the Genus *Cucumis* (Cucurbitaceae). Parkway publishers, Boone (NC, US)

Manniche L (1989) An ancient egyptian herbal. University of Texas Press, Austin

Meirano V (2000) Mets et végétaux en Grande Grèce: nouvelles données de la coroplathie. *PALLAS* 52: 167–180

Moldenke HN, Moldenke AL (1952) Plants of the Bible. The Ronald Press Company, New York

Naudin C (1859) Essais d'une monographie des espèces et des variétés du genre *Cucumis*. *Ann Sci Nat* 11: 5–87

Pitrat M (2008) Melon. In: Prohens J, Nuez F (eds) *Handbook of Plant Breeding, vol Vegetables I: Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae*. Springer, Heidelberg, pp 283–315

Schoske S, Kreissl B, Germer R (1992) "Anch" Blumen für das Leben. Pflanzen im alten Ägypten, vol 6. Schriften aus der Ägyptischen Sammlung. München

Sebastian P, Schaefer H, Telford IRH, Renner SS (2010) Cucumber (*Cucumis sativus*) and melon (*C. melo*) have numerous wild relatives in Asia and Australia, and the sister species of melon is from Australia. *Proc Natl Acad Sci USA* 107: 14269–14273

Serres-Giardi L, Dogimont C (2012) How microsatellite diversity helps to understand the domestication history of melon. In: Sari N, Solmaz I, Aras V (eds) *Cucurbitaceae 2012. Proceedings of the Xth EUCARPIA Meeting on Genetics and Breeding of Cucurbitaceae*, Antalya (TR), 15–18/10/2012. Çukurova University, pp 254–263

Stol M (1987) The Cucurbitaceae in the cuneiform texts. *Bull Sumer Agric* 3: 81–92

Tanaka K, Akashi Y, Fukunaga K, Yamamoto T, Aierken Y, Nishida H, Long CL, Yoshino H, Sato YI, Kato K (2013) Diversification and genetic differentiation of cultivated melon inferred from sequence polymorphism in the chloroplast genome. *Breed Sci* 63: 183–196

Vavilov NI (1957) The origin, variation, immunity and breeding of cultivated plants. *Chron Bot* 13: 1–366

Vishnu-Mittre (1974) Palaeobotanical evidence in India. In: Hutchinson J (ed) Evolutionary studies in world crops. Cambridge University Press, Cambridge, pp 3–30

Walters TW (1989) Historical overview on domesticated plants in China with special emphasis on the Cucurbitaceae. *Econ Bot* 43: 297–313