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Domestication and diversification of melon

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Abstract

As for 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... Other phenotypic traits are dominant (orange flesh colour, netting, yellow colour of mature fruit in the Amarillo type...) 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.

INTRODUCTION

Melon (*Cucumis melo*) is a polymorphic species cultivated in many countries with a hot season. Even if leaves are consumed in some places, it is mainly cultivated for its fruits. Wild melons can be found in Africa or Asia. But what is a “wild” melon? The word “wild” can be used as the opposite of “domesticated” or of “cultivated” which are not synonymous. Domestication is the status of co-evolution or co-adaptation or co-dependence of a plant and human beings. In other words, since the Neolithic revolution and the development of agriculture, man is dependent from domesticated plants for his food and the plant is dependent from man; without agriculture, a domesticated plant cannot survive in competition with weeds. A “domestication syndrome” (Hammer 1984) has been defined and studied in a few crops, mainly cereals (rice, barley, wheat and maize): seed dormancy, fragile or tough rachis (shattering), plant structure, inflorescence structure can be cited

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along with larger leaves or fruits or seeds, change in reproduction mode (autogamy *versus* allogamy)... All cultivated plants are not domesticated: for instance many forage grasses can survive in natural meadows. But melon, like most other fruits and vegetables has a low fitness to survive without man care and good horticultural practices and can be considered as domesticated.

Diversification or crop improvement corresponds to the different cultivars, cultigroups, botanical varieties which have been selected since the beginning of agriculture until now in different places in the world. In the case of melon, which is a plant domesticated since a long time, a large phenotypic diversity can be observed today, even if some types cultivated in some places many centuries ago are now extinct.

There is no clear limit between "domestication" and "diversification" but instead a continuum. Indeed many traits found in present day cultivars can be found in present day wild melons; for instance green flesh, monoecious or 3 placentas are observed wild melons and in some cultivars and the opposite traits (orange flesh, andromonoecious or 5 placentas) cannot be considered as domestication traits.

In some cases, escape from the "domesticated" status and return to the "wild" status can be observed. These populations are called "feral" and can be observed for instance in places which are not the centre of origin of the species. In the case of melon, the wild melon growing in Central America can be considered as feral. Their study in comparison with the wild types can bring interesting complementary data.

The wild types observed today are not the ancestors of the cultivated types. Indeed what we observe today is, for the wild melons, the result of natural selection from the ancestor and, for the cultivated melons, the result of artificial or man-driven selection (= domestication and diversification) from the ancestor.

In the case of vegetables, there are almost no archaeological data. Some pictures are available but are only a few centuries old (mainly from the European Renaissance) and do not represent the world diversity.

In this paper, I will try to identify some traits of domestication or diversification of melon and what is known on their genetic control.

WILD MELONS

As for many crops, there is a low phenotypic diversity in "wild" melons compared with the large phenotypic diversity of "cultivated" melons. Typical wild melons can be described as plants with small leaves. They are monoecious, with small flowers and small smooth oval-shaped fruits often light green with dark green dots or stripes, sometimes uniform light green. The flesh is very thin, light green often bitter with three placentas. Seeds are small, embedded in a gelatinous sheath and there is no seed cavity. Maturation can be climacteric or non-climacteric.

Several species such as *Cucumis pubescens*, *Cucumis trigonus* or *Cucumis*

turbinatus are now considered as wild types (and synonym) of *C. melo*.

Wild melons can grow close to field of cultivated melons in Africa or in India for instance. As they are allogamous, pollination can occur between both of them. This gene flow results in intermediate or recombinant types for instance the presence of sutures or light orange flesh.

In Central America and the Caribbean Islands, one can find small melons round or slightly oval with a yellow skin. The flesh is thin, light green or white and there is no seed cavity. Seeds are small and embedded in a gelatinous sheath. Plants are monoecious. In short, except for the yellow colour of the fruit exocarp, they look like "wild" and have been described under the name *chito* (Naudin 1859). America is not the centre of origin of melon. These genotypes could result from gene exchange between wild types brought from Africa (by slaves?) or Asia and cultivated melons. They could also represent feral accessions i.e a return to a wild status from the cultivated melons introduced in the New World.

Two sub-species have been described in *C. melo*: 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 been used earlier to describe the tribe of "wild" melons (Naudin 1859). A lot of confusion has resulted from these two meanings as the wild melons ("agrestis" *sensu* Naudin) can 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.

DOMESTICATION TRAITS

Phenotype

It is surprising to observe that, in the vicinity of fields where melons are cultivated, wild types remain quite typical despite repeated pollination (back-crosses!) by cultivars. For instance in Sudan, where *flexuosus* type is commonly cultivated, the wild melons have no elongated fruits.

As mentioned above, domestication traits have not been studied in vegetables and particularly in melon. A character often observed in many plants is the seed dormancy in wild types opposed to the absence of dormancy in cultivars. It can be easily understood that a negative selection has been applied by farmers for seed dormancy because they want that all the seeds germinate at the same time and not for several years in one field. Seed dormancy of wild melons has not been clearly described but it is a common observation in seed banks that wild accessions have a low germination rate.

Compared with wild melons, modern cultivars are characterized by large, non-bitter fruits with a thick flesh and large seeds. Most of the other traits of wild melons like sex expression, fruit shape, fruit colour, flesh colour, sugar, aroma... have been conserved in some cultivars and must be considered as diversification

and not as domestication characters.

The most typical trait of domestication i.e. the loss of fitness or competitiveness towards weeds has not been analysed in any plant and is poorly understood.

Domestication events

There is no definitive answer to the number of domestication events. The existence of two sub-species and the fact that wild types can be found in the two sub-species are strong arguments in favour of two independent domestication events. The presence of the same phenotypic traits in both sub-species, for instance, sex expression, fruit size and shape, fruit flesh colour, sugar, some disease resistance like *Fusarium oxysporum* f.sp. *melonis* race 1 or race 2 can be explained by the appearance and the selection of the same trait in independent lines or by gene exchange between lines. The general picture is that sub-species *agrestis* is found from India to Far-East with the types *momordica*, *acidulus*, *conomon*, *momordica*, *chinensis*, and the sub-species *melo* in India and west of India (central and western Asia, Africa, Europe and America) with the types *cantalupensis*, *inodorus*, *reticulatus*, *ameri*, *flexuosus*, *chate*, *dudaim*... The exceptions are the *chito* in America and the *tibish* in Africa. The *chito* case has been discussed above and in the case of *tibish*, it could correspond to a third domestication event.

Where and when the domestication event(s) occur(s) is not known. Data on the existence of cultivated melon in ancient time are scarce (Moldenke and Moldenke 1952; Andrews 1956; Keng 1974; Vishnu-Mittre 1974; Stol 1987; Manniche 1989; Walters 1989; Schoske et al. 1992; Decker-Walters 1999; Meirano 2000). The main conclusion is that melon was probably cultivated more than 2000 years BCE.

DIVERSIFICATION TRAITS

The large phenotypic diversity of modern cultivars is the result of positive or negative selection by farmers during the millennia of domestication and diversification. A non exhaustive list of the characters follows.

Fruit size and shape

Fruit shape can vary from flat to very long (up to 1.8 m) in the *flexuosus* group. Fruit weight is commonly between 1 and 2 Kg but smaller (200-300 g) to larger (more than 5 Kg) fruits can be observed, compared with 20-50 g of wild melons.

Fruit exocarp

Primary and secondary fruit colours are white, bright yellow, orange, brown, light green, dark green. The pattern can be uniform (honeydew, Amarillo, Yuva), with dots (Piel de sapo, Kırkağaç) or stripes (*dudaim*). Sutures can be present (Charentais, Ogen) or not. Exocarp can be netted (*reticulatus*) or wrinkled (Tendral).

Fruit flesh

Flesh colour can be white, green or orange. It can be noted that no red-flesh melon with high lycopene content (like in watermelon) has been selected. Melon fruits can be sweet (*cantalupensis*, *reticulatus*, *inodorus*...) or not (*acidulus*, *flexuosus*, *conomon*...). Texture varies from mealy (*momordica*) to juicy (Ananas) to firm and crispy (*acidulus*). Many volatile compounds have been identified: *dudaim* represents a highly aromatic type and *acidulus* or *conomon* a non-aromatic type. Some types are characterized by 5 placentas (*dudaim*, *conomon*, *chinensis*) instead of 3 (*cantalupensis*, *inodorus*).

Seeds

Seed size can be up to 10-12 seeds, compared to 290 seeds per gram for wild types, a more than 20-fold increase. Seed colour can be white, yellow or brown. Seeds can be embedded or not in a gelatinous sheath.

Sex expression

A majority of cultivars is andromonoecious and a few accessions from China are hermaphrodite.

Leaves and roots

A large variability exists in leaves shape, size and colour from light green to dark green, in stem diameter and also in root architecture from many superficial small roots to a few very large roots.

Adaptation to climactic conditions

Cultivars have been selected in area with different soil and climatic conditions. They can be adapted to dry, sandy soil and high temperature (warm desert) to lower temperature and more humid conditions (semi-continental).

Disease and pest resistance

Wild accessions are generally susceptible to most of the viruses, bacteria, fungi, insects, nematodes that can attack melons. May be there is a bias because few wild accessions maintained in the collections have been evaluated. Among the resistances identified in wild accessions, resistance to PRSV-W (in PI 180280 and PI 180283) and to *Dacus cucurbitae* (in *Cucumis callosus*), one of several sources of resistance to *Didymella bryoniae* (PI 140471) or to *Acidovorax avenae* subsp *citrulli* (PI 536473) can be cited. In contrast, in some cultigroups resistance to many diseases has been identified, for instance to powdery and downy mildew in the *momordica* and *acidulus* types from India, to *Cucumber mosaic virus* (CMV) and *F. oxysporum* f.sp. *melonis* race 1.2 in the *conomon* and *makuwa* types from Far-East.

Of course many mutations with "negative" effect which are now maintained in gene banks have not been selected by farmers: chlorophyll deficiency, male-sterility, nectarless...

GENETIC CONTROL

What is the genetic control of these different traits? To study the inheritance of 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. One inconvenient of this approach is that the dominance or recessivity of each detected QTL cannot be estimated.

Recessive genes and QTLs

Absence of bitterness in the fruit is maybe one domestication trait and the absence of cucurbitacins in the plant and/or the fruit is controlled by recessive alleles at several loci (Bi^+ , $Bif-1^+$, $Bif-2^+$, $Bif-3^+$).

Andromonoecy is controlled by the recessive allele a and hermaphroditism by the two recessive alleles a and g . Regarding some fruit characters, presence of sutures (allele s), uniform colour (alleles Mt^+ , spk , st), white colour of mature fruits (allele w), white flesh colour (allele wf), absence of gelatinous sheath around the seeds (allele Gs^+) are recessive genes.

Resistance to *Melon necrotic spot virus* (MNSV, allele nsv), to *Cucumber vein yellowing virus* (CVYV, allele $cvy-2$), to *Cucurbit aphid borne yellows virus* (alleles $cab-1$ and $cab-2$) or polygenic resistance to CMV or *F. oxysporum* f.sp. *melonis* race 1.2 are also controlled by recessive genes.

Dominant genes and QTLs

There are also some dominant genes or QTLs present in cultivated types.

Orange flesh colour (allele gf^+), yellow colour of mature fruit (allele Y), netted fruit exocarp or andromonoecy in *tibish* type are controlled by dominant genes. Many pest and disease resistance are also controlled by dominant genes: *F. oxysporum* f.sp. *melonis* races 1 or 2 (allele $Fom-1$ and $Fom-2$), *Aphis gossypii* (allele Vat), powdery mildew (several loci and alleles), *Alternaria cucumerina* (allele Ac), *D. bryoniae* (several loci), *Papaya ringspot virus watermelon type* (PRSV-W, locus Prv), *Zucchini yellow mosaic virus* (allele Zym), CVYV (locus $Cvy-1$)...

Recessive versus dominant

Compared with the phenotype of a typical wild melon, most of the genes and QTLs controlling traits in cultivars are recessive, except disease resistance (Lester 1989). Recessive genetic control corresponds often to non-functional

proteins whatever the cause: point mutation, stop codon, transposon insertion... Nevertheless, the loss or decrease in function does not indicate a reduced trait but can correspond to an increase or a hypertrophy. For instance the decrease of a hormone level can result in larger fruits resulting from an increase of cell numbers or of cell sizes. When an ACC synthase gene (*CmACS-7*) is active with production of ethylene, there are no stamens in the female flowers; when this enzyme is inactive, corresponding to the allele *a* (andromonoecy), stamens are present in female flowers (Boualem et al. 2008).

In contrast, more resistances under dominant genetic control compared to the wild type than under recessive control have been identified. A dominant resistance is usually an active mechanism induced in the interaction plant * pathogen while a recessive one is usually constitutive and corresponds to a lack of function necessary for the pathogen. The cost in term of fitness for a permanent loss corresponding to a recessive control could be higher than the temporary induction of a mechanism only at the time of contact with a pathogen.

Parallel evolution?

For most of the phenotypes listed above, the mutant trait, compared with the wild type, is observed in both sub-species; for instance andromonoecy in *cantalupensis*, *reticulatus* or *dudaim* in sub-species *melo* and in *conomon* or *makuwa* in sub-species *agrestis*; Fusarium wilt race 1 or race 2 or MNSV resistance in both sub-species... Did this phenotypic trait appear only one time and spread in the different present-day cultigroups by intercrossing or did this trait appear independently several times in the cultigroups? For a monogenic trait both hypothesis can be true. For polygenic traits such as high sugar content, fruit size, some resistance (CMV, *F. oxysporum* f.sp. *melonis* race 1.2) the first hypothesis is more probable.

Polygenic recessive traits are more probably the result of domestication (long term selection by man) while monogenic traits can appear in hot-spots of diversity: for instance many genes for pest and disease resistance are found in different types, mainly *momordica* and *acidulus*, in India.

MOLECULAR DATA

There are few data on the allelic diversity of genes with a phenotypic effect controlling domestication or diversification traits.

Wild melons are monoecious while about 2/3 of cultivars are andromonoecious. This last phenotype is controlled by a single point mutation which codes for a deficient ACC synthase. Eleven haplotypes for the allele *a*⁺ have been described and only one haplotype for the allele *a* controlling andromonoecy. This last allele is present in many melon types from different geographical origins. The different haplotypes of the *a*⁺ allele are not clearly related with geographical origin or with

botanical groups (Boualem et al. 2008).

Wild melons are susceptible to MNSV and resistance has been described in several accessions from Far-East or USA. The *nsv* locus encodes for the translation factor eIF4E and resistance corresponds to a single point mutation (Nieto et al. 2006). Six haplotypes have been described but there was no general relationship with geographical origin (Nieto et al. 2007).

CONCLUSION

Wild and cultivated melons differ by many traits but very little is known on the genetic control of the domestication characters. It is also the case of other vegetables compared with cereals. Absence of fruit bitterness and large fruit size are two traits which have been studied but there are no data on other traits probably involved in domestication such as seed dormancy or fitness in non-horticultural conditions. It is not clear how many independent domestication events give way to the present day cultivated melons. Based on the two sub-species and the isolated position of *tibish* group, one can speculate on three domestications; the *chito* type could correspond to a feral melon.

Concerning the diversification characters, most of them are under recessive control which does not mean a loss of a trait. Many traits are present in different botanical groups such as flesh colour, sutures, sex expression, some disease resistances. It corresponds to parallel evolution i.e. the appearance of one phenotypic trait in genetically independent lineages. But it could also result from intercrossing and migration.

As soon as a gene with a phenotype involved in domestication and/or diversification is identified, the allelic diversity of this gene could be studied by eco-TILLING or by resequencing. In the next years, we will have a better understanding of the evolution of melon.

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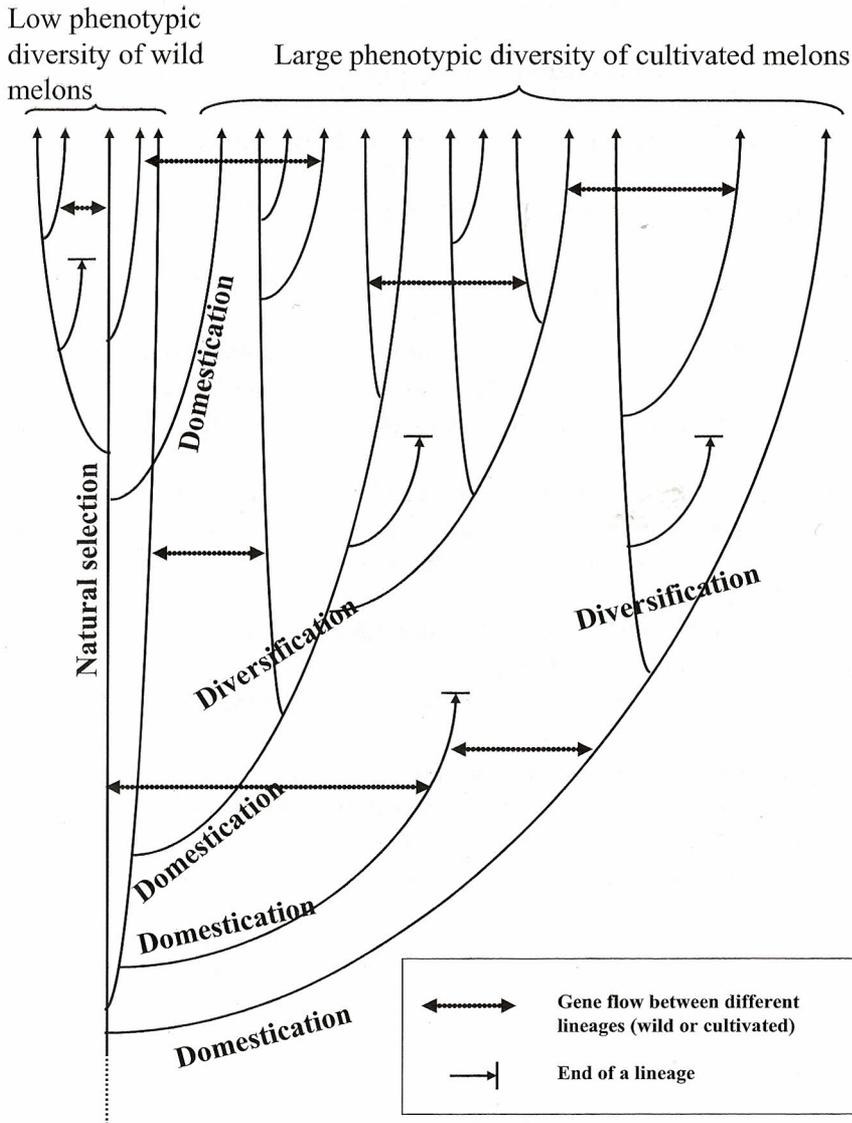


Fig. 1. Schematic representation of the effect of natural selection (left) and domestication/diversification (right). The bottom to top represents time from the first domestication to present day. Four independent domestication events are represented but one ends before producing modern varieties. Gene flow results from intercrossing between wild and/or cultivated types at places where different types (wild and/or cultivated) are present. Domestication represents the first step from the wild status and is followed by diversification or selection of different cultivated types. Domestication and diversification are not clearly separated but represent a continuum.