C. R. Biologies xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Comptes Rendus Biologies

www.sciencedirect.com

Trajectories of genetics, 150 years after Mendel/Trajectoires de la génétique, 150 ans après Mendel

Superheroes and masterminds of plant domestication

La domestication des plantes : une affaire de super-héros et de masterminds

Natalia E. Martínez-Ainsworth, Maud I. Tenaillon *

Génétique Quantitative et Évolution–Le Moulon, INRA, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, 91190 Gif-sur-Yvette, France

A R T I C L E I N F O

Article history:
Received 5 April 2016
Accepted after revision 24 April 2016
Available online xxx

Keywords:
Domestication syndrome
Human-mediated selection
Convergent evolution
Pace of domestication
Bottleneck
Gene flow

Mots clés :
Syndrome de domestication
Sélection humaine
Évolution convergente
Tempo de la domestication
Goulot d'étranglement
Flux de gènes

A B S T R A C T

Domestication is one of the most fundamental changes in the evolution of human societies. The geographical origins of domesticated plants are inferred from archaeology, ecology and genetic data. Scenarios vary among species and include single, diffuse or multiple independent domestications. Cultivated plants present a panel of traits, the "domestication syndrome" that distinguish them from their wild relatives. It encompasses yield-, food usage-, and cultivation-related traits. Most genes underlying those traits are "masterminds" affecting the regulation of gene networks. Phenotypic convergence of domestication traits across species or within species between independently domesticated forms rarely coincides with convergence at the gene level. We review here current data/models that propose a protracted transition model for domestication and investigate the impact of mating system, life cycle and gene flow on the pace of domestication. Finally, we discuss the cost of domestication, pointing to the importance of characterizing adaptive functional variation in wild resources.

R É S U M É

La domestication est l'un des changements les plus fondamentaux dans l'évolution des sociétés humaines. Les origines géographiques des plantes domestiquées sont inférées à partir de données archéologiques, écologiques et génétiques. Les scénarios de domestication varient d'une espèce à l'autre et comprennent des exemples de domestication unique, diffuse ou de domestications multiples et indépendantes. Les plantes cultivées présentent un panel de caractères, le « syndrome de domestication », qui les distingue de leurs apparentés sauvages. Ce syndrome englobe des caractères liés au rendement, à l'utilisation et à la facilité de culture. La plupart des gènes qui sous-tendent ces caractères sont des *masterminds* affectant la régulation des réseaux de gènes. La convergence phénotypique des caractères de domestication, qu'elle soit présente entre différentes espèces ou au sein d'une espèce entre des formes domestiquées indépendamment, coïncide rarement avec une convergence au niveau des gènes. Nous synthétisons ici les données et modèles actuels, qui proposent un modèle de transition prolongée des formes sauvages vers les formes cultivées, et s'intéressent à l'impact du

* Corresponding author at: Ferme du Moulon, 91190 Gif-sur-Yvette, France.
E-mail address: tenaillon@moulon.inra.fr (M.I. Tenaillon).

http://dx.doi.org/10.1016/j.crvi.2016.05.005

système de reproduction, du cycle de vie et des flux géniques sur le tempo de la domestication. Enfin, nous discutons le coût associé à la domestication, qui souligne l'importance de caractériser la variation fonctionnelle adaptative présente dans les ressources génétiques sauvages.

1. Introduction

Since their origin, hunting and gathering had been the primary mode of subsistence for modern humans. But around 12,000 years ago, humans switched from a hunter-gatherer lifestyle to an agricultural lifestyle. This transition in human behavioural ecology is known as "the Neolithic revolution". The Neolithic revolution has marked one of the most profound changes in human evolution. With reliable food stocks, human populations have increased, expanded, and built civilizations with environmental and cultural consequences that persist today. One of the primary drivers of this transition is the domestication of plants, a process whereby wild plants have been evolved into crop plants through human-mediated selection. Plant domestication has entailed co-dependency between humans and plants while promoting plant adaptation to a new ecological niche, the field. How complex were domestications? Where did they take place? How long did they last? These are some of the questions at the interface between archaeology, ecology and evolutionary genetics that have been until today actively debated, starting with the observations of Charles Darwin first published in 1868 in a book entitled "The Variation of Animals and Plants under Domestication".

2. What is plant domestication?

Domestication can be described as a set of consecutive stages that begins with the onset of domestication followed by an increase in the frequency of a set of desirable traits (the domestication traits), and which culminates with the emergence of cultivated populations adapted to both human needs and a cultivated environment. Thereupon a first challenging task is to define a domestication syndrome, which is the subset of traits that collectively form the morphological and physiological differences between crops and their wild progenitors. Domestication traits were the very first targets of early farmers as opposed to traits selected later during crop diversification. We expect them to be fixed or nearly fixed in the cultivated forms as a result of intense human-driven positive selection.

Domesticated traits can be classified into three categories:

- yield-related traits that affect propagule retention, shape and size – longer and more rigid stolons in cultivated potatoes, loss of seed shattering in cereals, indehiscent pods in legumes, increase in fruit size of cultivated tree species are some examples;
- food usage-related traits such as reduction of chemical and physical defences, and reduction of propagule ornamentations that facilitate dispersal in the wild – loss of bitterness in cultivated almonds, loss/reduction of awns in rice and wheat fall in this category;
- cultivation-related traits that concern growth habit and loss of seed dormancy – the determinacy in bean cultivated forms and loss of seed dormancy in chickpea illustrate this last category.

Domesticated plants often rely on human maintenance to ensure their reproductive success, and domesticated traits are usually highly deleterious in the wild environment. For instance, propagule dissemination or seed dormancy are essential for survival in the wild but selected against in the field.

3. Single versus multiple domestications

At least 11 regions of the Old and New World can be considered as independent isolated centres for the origin of crops, several of which occur in Central and South America, Africa, and South East Asia [1]. The Fertile Crescent is considered as the cradle of plant domestication with the emergence of major cereals such as wheat, barley, oats, rye, as well as lentils and chickpeas. Some of the related wild forms of these crops were cultivated before domestication. Hence Weiss et al. [2] have reported consistent evidence of granaries containing hundred thousands of wild barley and oat seeds in the Jordan Valley, suggesting seed management and perhaps mass-selection predating domestication.

While attempting to determine the origins of crops using genetic data, it is not uncommon to arrive at conflicting interpretations. Recurrent gene flow among cultivated forms or between wild and cultivated gene pools, for instance, may mask multiple domestication events. It is therefore important to merge multiple sources of data and assess congruence between archaeological findings and genetic analyses. Paleoclimatic reconstructions may also guide inferences on the ancient niches occupied by wild progenitors as reported for teosinte/maize landraces by Hufford et al. [3]. Along the same line Kraft et al. [4] have integrated evidence from paleobiolinguistics – the presence of words designating the cultivated species in an ancestral language being indicative of its importance – as a geographical grid layer complementary to that of genetic diversity and environmental niche projections in order to help refine the