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Unconscious Selection and Domestication in "Wild-type" *Arabidopsis thaliana* (Brassicaceae)

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ABSTRACT

We propose that the two commonly used "wild type" *Arabidopsis thaliana* cultivars, *Landsberg* and *Columbia* became unconsciously domesticated. The conditions used for growing *A. thaliana* for research are very different from the natural conditions near Landsberg, Germany from where they originated. Laboratory practices for dozens of generations must have selected for characters that give *Arabidopsis* advantages under laboratory growth conditions and against ones beneficial in the wild but with reduced fitness in laboratory "ecosystems". From what we already know about unconscious selection in agriculture, we can infer that these so-called "wild types" have been changed into laboratory organisms that are inherently different from the native wild type. Because of the detailed genetic knowledge of *A. thaliana*, these genotypes can be used to study processes of unconscious selection more precisely than any other plant.

Keywords: *Columbia*, laboratory organism, *Landsberg*

INTRODUCTION

The establishment of agriculture in the Near East about 11,000 years ago, and later in other regions, was one of the crucial events in human history, leading to an explosion in world population and the emergence of modern civilization (Diamond 1997; Lev-Yadun *et al*. 2000). However, many fundamental biological aspects of the domestication of wild crop species (the transition from wild progenitors to domesticated crops) are still poorly understood. A better understanding of the biology of the process may enhance the modes of crop improvement and future domestications. Differences between an agricultural crop or a weed and its wild progenitor are usually studied using progeny of crosses between the wild type and the crop or weed (see review in Ladizinsky 1998). As for the extent of influence, analysis of single-nucleotide polymorphisms in 774 *Zea mays* genes indicated that 2-4% of them experienced artificial selection since the domestication of the wild maize progenitor teosinte, accounting for about 1,200 affected genes in the whole genome (Wright *et al*. 2005).

UNCONSCIOUS SELECTION

Automatic selection (Harlan 1975) also known as unconscious selection (Harlan *et al*. 1973; Zohary 2004) has played a major role in plant domestication and in the evolution of weeds (Barrett 1983). Agricultural practices form a new ecosystem, in which certain traits are selected either for or against (Harlan 1975; Ladizinsky 1998). Harlan (1975) and Ladizinsky (1998) listed major genetic characters that automatically change in crops or weeds when exposed to an agricultural regime. These include: non-shattering of seeds, more determinate growth, stronger apical dominance, fewer and larger inflorescences, larger seed, uniform ripening, greater or lesser day length sensitivity, high or low temperature response (including vernalization sensitivity or insensitivity), synchronous tillering and uniform whole plant maturation, increase in percent seed set, sterile flowers become fertile, alterations in protein and carbohydrate content, loss of germination inhibition, loss of toxicity, changes in coloration, reduced competitive ability with wild plants and increased competitive ability with cultivated plants. The conditions that result in unconscious selection in crops and weeds vary a great deal. The climate, soil, water economy, season of growing, methods of tilling the soil, harvesting, etc. differ from crop to crop or may differ within the same crop in different locations. Thus, there is no single pattern of unconscious selection but rather a large set of "unconscious selections". We propose here that new insights into the process of unconscious selection are probably within reach using *Arabidopsis thaliana* as a model for the study of these questions.

"WILD TYPE" *ARABIDOPSIS THALIANA*

The two commonly used "wild type" *A. thaliana* cultivars, *Landsberg* and *Columbia* (Koncz and Rédei 1994), originated from wild material from Landsberg (Germany). The material was collected by Professor Laibach in the early 1950's, sent to Professor Györffy in Hungary in 1955, and brought to Columbia (Missouri, U.S.A.) by Rédei in 1956 (Rédei 1992). There is sound genetic evidence that a considerable genetic bottleneck occurred when *A. thaliana* was collected from the wild and following further selections, especially when single seeds were harvested from each plant (Pigliucci 2003; Koorneef *et al*. 2004; Schmuths *et al*. 2004). Genetic bottlenecks are not unusual for crops selected for domestication (Ladizinsky 1998). The conditions used for growing *A. thaliana* for research are very different from the natural conditions near Landsberg, Germany, and are much more constant and controlled. Indeed, recently Lev-Yadun and Berleth (2009) proposed that the natural conditions have to be recorded when *A. thaliana* accessions are collected in the wild. Laboratory practices include seed sterilization; germination on agar or sterilized mixtures of peat, vermiculite or similar substrates rather than the original type of soil; different soil microorganism flora; cons-

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Research Note

tant temperature or otherwise un-natural temperature regimes; illumination that differs in photoperiod, spectrum, intensity and constancy; improved mineral nutrition; closed growth containers that could cause alterations in gas mixtures including increases in ethylene and oxygen and decreases in CO_2; high density of seedlings; lack of competition with other plant species; spraying against pathogens; lack of exposure of seeds or plants to very low winter or spring temperatures (even when vernalized); break-down of partial seed dormancy in the wild type; increased inbreeding within a sibling population without occasional introgression; and probably changes in additional factors. A considerable measure of unconscious selection must have occurred for characters that give *Arabidopsis* advantages under laboratory growth conditions and against ones that may be beneficial in the wild but reduce fitness in laboratory "ecosystems". Inbreeding should have also affected its biology as heterosis occurs with crosses of various accessions (Bustamante *et al*. 2002; Rohde *et al*. 2004). All these conditions differ largely from the conditions in its natural habitats (see Hoffmann 2002). From what we already know about unconscious selection, we can infer that the *Colombia* or *Landsberg* "wild types" have been changed into laboratory organisms that are inherently different from the native wild type.

NUMBER OF GENERATIONS UNDER DOMESTICATION

Although the number of generations probably differs among *A. thaliana* seed lots, many generations must have passed since the original collection from the wild almost 60 years ago. All our attempts to recover the exact or even estimated number of generations that have passed since *A. thaliana* was collected from the wild were unsuccessful. The Arabidopsis Stock Center (ABRC, Ohio State University, Columbus, OH) does not have such records. Assuming two generations per year, some "wild type" material has probably passed 100 generations under laboratory conditions. Contrary to annual field crops that have passed thousands of generations under domestication, in fruit trees the number of generations that have passed since domestication is usually small. Cuttings of various types or grafting are used to clone fruit trees (Zohary and Hopf 2000), and such cloned varieties may be retained for centuries if not millennia. Therefore, the number of generations separating the current domesticated fruit-tree cultivars from the wild progenitors is small, probably less than 10 generations in some species and not more than a few dozen in others. The long history of *A. thaliana* (in terms of the number of generations) as a laboratory organism and the unconscious selection forces, either for or against various characters that adapt it to laboratory conditions, that must have operated on the laboratory populations seem to meet the criteria for considering *Columbia* and *Landsberg* as domesticated. The vast knowledge of the genetics of *A. thaliana* (e.g., The Arabidopsis genome initiative 2000) may enable a detailed understanding of the processes of unconscious selection that operated on it, which, in turn, will illuminate these issues in classic crops.

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