Pulse Domestication before Cultivation[1]

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Comparative studies of the pulses of the Middle East and of their wild progenitors indicate that the pattern of pulse domestication is completely different from that of cereals in the same region. Wild legumes are not suitable for cultivation because of their conspicuous seed dormancy. Pre-adaptation of wild pulses for cultivation through loss of the seed dormancy mechanism apparently occurred in wild populations and may have been influenced by the gathering practices of man in pre-agricultural times. Pod indehiscence was of low value in pulse domestication and had evolved after the crop was well established and widespread.

It is generally accepted that wild forms gave rise to our crop plants. However, the process by which these wild plants were domesticated is not yet fully understood. It is also a basic premise that, prior to domestication, man utilized wild plants by gathering them from their natural habitats.

Zohary (1969) thus disinguished between this gathering stage and the domestication stage, when man intentionally planted and harvested his crops. Harlan (1975), on the other hand, made a clear distinction between cultivation, which includes all necessary activities related to crop management, and domestication, which is an alteration of morphological and genetic characteristics of wild plants or animals that make them better adapted to the ecological environment created by man. On an evolutionary scale, domestication is a recent event, and therefore the main steps of this process can be identified and reconstructed. In a given crop plant such identification and reconstruction are conditioned by availability of the wild ancestor for comparative studies of traits modified under domestication. Identification of the wild ancestor is based on general morphological similarity and on high or complete interfertility with the crop plant. Clues regarding the major steps in domestication can be obtained by examining plant remains from archeological digs.

In the last 2 decades our ideas regarding plant domestication have evolved mainly from comparative studies of cereals that originated in the Middle East and of their wild progenitors. Wild progenitors of some legumes of that area have recently been identified and confirmed (Ben Ze'ev and Zohary 1973; Ladizinsky and Adler 1976; Ladizinsky et al. 1984), thus enabling more comprehensive views on plant domestication in the Middle East. Because genetic differences between cultivated and wild forms are better known in lentil than in other food legumes, it will be used to demonstrate some of the main features of pulse domestication.

The wild lentil, *Lens orientalis* (Boiss.) M. Popov, has been identified as the wild progenitor of the cultivated lentil, *L. culinaris* Medik. (Ladizinsky 1979a). This wild species is dispersed sporadically from Turkey to Uzbekistan, but is restricted to stony habitats and shallow soil, particularly at high elevations. It usually forms small populations in sparse stands. The plants are small (5–25 cm), and highly self-pollinated, producing few pods, each containing one or two seeds.

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TABLE 1. SEED CHARACTERISTICS OF THREE POPULATIONS OF *L. ORIENTALIS*.

Population	No. seeds/plant	Weight of 100 seeds	% germination[a]
Jerusalem	10.5 + 8.9	1.07	12.2
Ein-Zeitim	9.9 + 6.3	0.84	9.1
Hermon	9.7 + 7.2	0.78	10.5

[a] Six mo after harvest.

The number of seeds borne by a single *L. orientalis* plant was estimated by us in three natural populations of this species in Israel. In each population, 50 plants chosen at random were collected by uprooting them when the lower pods were already dehiscing or just before. The number of seeds lost by shattering was thus reduced, but the immature pods yielded inviable seeds. The number of seeds per plant was low (Table 1) but a great variability in this number (1–45) among plants was observed, which probably resulted from the diverse micro-niches where the individual plants grew. In these populations the weight of 100 seeds was about 1 g or less (Table 1). Assuming that, on an average, 10 seeds can be collected from one plant, about 10,000 plants are required in to provide 1 kg of clean seeds. The low seed productivity of *L. orientalis* in its natural habitat indicates that, in pre-agricultural times, gathering lentil seeds was a difficult task, and lentils apparently constituted a negligible part of the human diet. The same is probably true also for wild peas and chickpeas as they, too, form small and disjunct populations in nature. This is in sharp contrast to the situation described for wild cereals of the Middle East. Harlan (1967), in 1 hr, was able to collect in Turkey an amount of wild diploid wheat equivalent to 1 kg of clean seeds, and Ladizinsky (1975) reported that in the upper Jordan Valley, and also in 1 hr, 0.5 kg of clean seeds of wild tetraploid wheat were collected.

Two main characteristics, seed dormancy and pod indehiscence, distinguish cultivated from wild forms in the food legumes. The genetics of these differences have recently been studied by us in lentils and have shed light on some aspects of domestication of lentils and perhaps of other food legumes.

SEED DORMANCY

Fresh seeds of *L. orientalis* do not germinate because of their hard seed coat. This dormancy remains effective for as long as 6 mo following dispersal, i.e., until the time of the germinating season in nature; only about 10% of the seed germinates then (Table 1). Moreover, the seeds we collected from plants originating from this small proportion of germinating seeds were dormant too, indicating that the sporadic germination of wild lentils is due to incomplete penetrance rather than to genetic polymorphism. The proportion of dormant seeds capable of germinating in the second year was estimated in one of the tested populations and was very low, about 7%.

In contrast, fresh seeds of most of *L. culinaris* lines germinate readily when appropriate moisture and temperature are provided. The difference in germination pattern is governed by a single major gene; the cultivated type is dominant (Ladizinsky 1985a).

It seems that seed dormancy has a considerable adaptive value in *L. orientalis.*

It regulates germination time and avoids extinction should effective rain at the beginning of winter be followed by a long drought. Secondly, it apparently controls population density. If all the seeds germinated during the first season, the population would become overcrowded and the limited resources of the natural habitat might become exhausted before the plants reached maturity. Theoretically a population of about 100,000 plants could be formed from a single seed of a dormancy-free mutant after 6 yr.

Because of this seed dormancy, sowing and harvesting of wild lentils must have been difficult and problematic. When about 10% of the sown seed germinates, and each germinating plant produces 10 seeds, the expected yield would be similar to the amount of sown seeds. The yield would not be improved significantly even if the same field was used for 2 consecutive years because only a small proportion of the dormant seeds would germinate the following year. Thus, from an input-output point of view the sowing of wild lentils is highly inefficient and provides no incentive for cultivation. The situation is no less complicated if one assumes that genetic polymorphism for seed dormancy might exist in wild populations of *L. orientalis.* In such a case seed-dormancy-free types would be kept at low frequency, and sowing seeds from such polymorphic populations would not appreciably affect the stand in the sower's field. In order to be more suitable for cultivation, wild lentils must have been pre-adapted by losing their full or partial seed dormancy. The dilemma, however, is how such pre-adaptation could be acquired under natural conditions where absence of seed dormancy is negatively selected.

A seed-dormancy-free mutant apparently can be established, at least temporarily, in a natural population of *L. orientalis* if most of the produced seeds are removed and a population explosion is thereby avoided. This could have occurred because of the gathering practices of man in pre-agricultural times.

When the mutation rate of the seed dormancy gene in lentil is 10^{-4} (the rate by which dormancy-free type is spontaneously formed), and each plant produces 10 seeds of which two are dispersed before gathering, the establishment of the mutant in the population would benefit by a consistent and massive gathering. Figure 1 shows that, theoretically, the proportion of the new allele will increase rapidly and might reach fixation after 7 yr. No less important is that, following a possible initial reduction in population size during the first few years, the population would regain its former numbers after about 14 yr. This event could occur independently in several populations of *L. orientalis,* and when the collected seeds were also used for sowing, those lacking dormancy would form better stands, produce higher yield, and constitute the seed stock for further sowing.

Seed dormancy due to seed coat hardness is common in wild peas and chickpeas but is absent in their cultivated counterparts (unpublished data). The genetic factors controlling these differences have not yet been studied, but it is a reasonable assumption that they are similar to the lentil; namely, that selection of seed-dormancy-free types was made in the wild, and not in cultivation, thus indicating that pulse domestication started before cultivation.

ROLE OF POD INDEHISCENCE IN PULSE DOMESTICATION

Mature pods of *L. orientalis* dehisce immediately when dry, ejecting the seeds up to a distance of 2 m; in most cultivated lentils the mature pods remain intact.

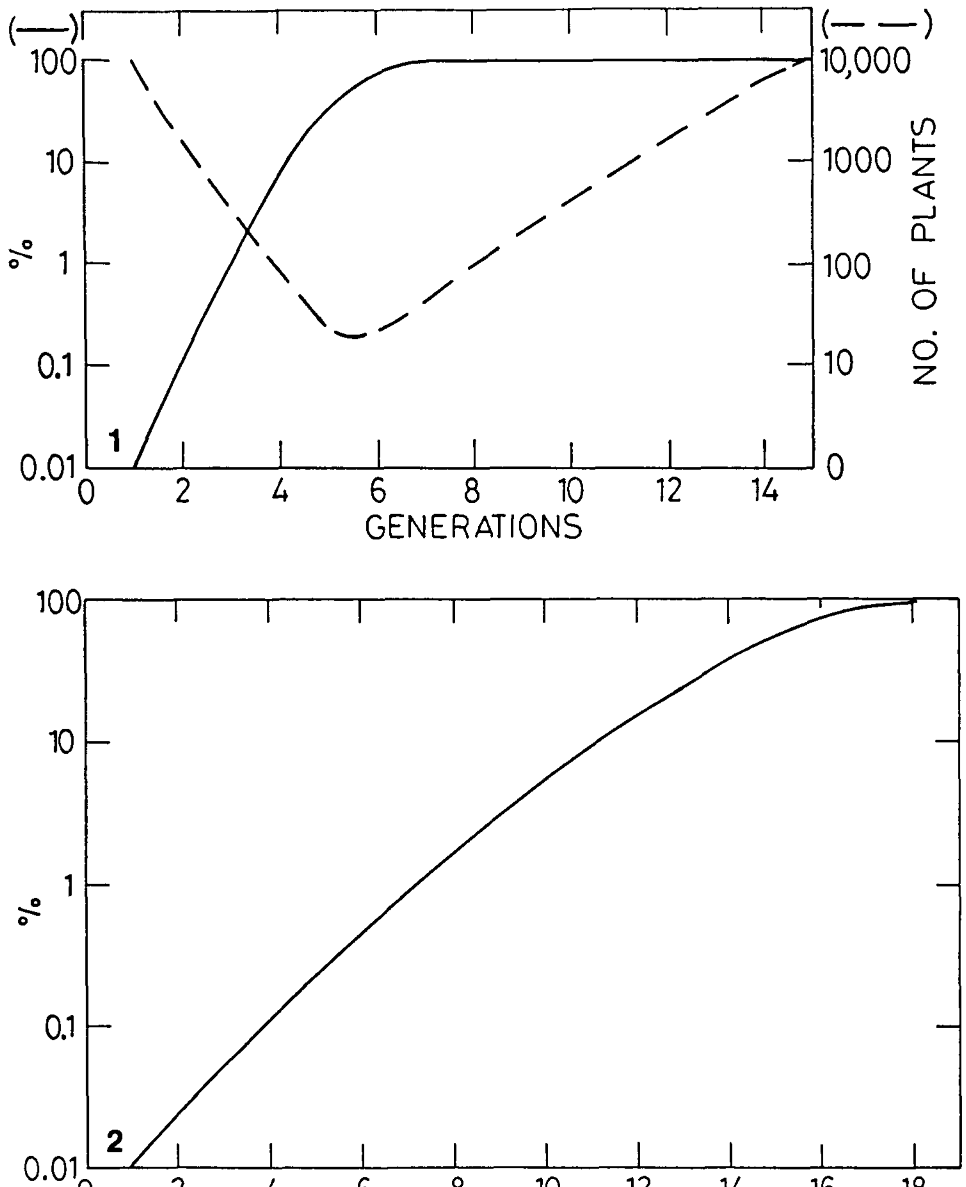

Fig. 1–2. Fig. 1. Theoretical increase of seed-dormancy-free type in natural population of *L. orientalis* as a result of massive gathering (solid line) and the resultant population size (broken line). Fig. 2. Accumulative figure of pod-indehiscent mutant in lentil as a result of 50% seed loss.

The difference between the two is controlled by a single Mendelian factor, and also perhaps a few modifing genes; the characteristic of the cultivated type is recessive (Ladizinsky 1979b). In an analogy to what has been proposed for wheat and barley (Harlan et al. 1973), one might assume that pod indehiscence in lentil, and perhaps in other legumes, has been favored in sowing-harvesting cycles. Traditional growing methods, however, indicate that this is apparently not the case since under these conditions pod indehiscence seems to be neutral. Lentils are harvested in many southwestern Asiatic countries and elsewhere by uprooting the mature but still partially green plants, sun drying them in heaps, and then threshing them on the spot. In such circumstances seed loss might occur only from late harvesting, but this is rarely the case because lentil is usually the first crop to be harvested in the area in which it grows. Severe loss by shattering could be expected when the harvested dry plants are moved from the field to the threshing ground, which is usually near the village. It is common practice in southwestern Asia to load dry lentil plants on donkeys and mules and carry them distances of several km. Occasionally this is done at night or early morning when relative humidity is high and pod dehiscence and seed loss are reduced, but such loss can still be enormous, thus favoring pod indehiscent types.

When the mutation rate of the pod dehiscence gene is 10^{-4} and the selection coefficient against the wild type is $S = 0.1$ (seed loss of 10%), the establishment of a mutant in a population of the domesticated lentil might be a very slow process and would be affected mainly by random drift. However, when $S = 0.5$, the proportion of the pod-indehiscent types would be doubled each year and eventually reach fixation after about 18 yr (Fig. 2). Even though random drift and yearly variation in seed loss might speed or slow down this process, it is on average fairly quick. Such a simplified model suggests that the pod-indehiscent mutant could be selected independently in different locations and at different times since it apparently occurred when the crop was well established and widespread. This supposition is strongly supported by recent evidence from isozyme electrophoresis. The cultivated lentil and *L. orientalis* share the same alleles in all the studied loci (Pinkas et al. 1985), while in other crop plants the cultivated forms usually have significantly fewer alleles per locus when compared with the wild progenitor (Ladizinsky 1985b).

It is now obvious that pulses and cereals in the Middle East underwent different patterns of domestication. Seed dormancy is common also in wild cereals. The dispersal unit of diploid and tetraploid wild wheats usually contains two kernels, the upper one germinating in the ensuing winter, the lower one a year later (Zohary 1969). In the wild oat *Avena sterilis* L., too, the dispersal unit contains two or three kernels and germination is distributed as in wild wheats, but in oats the lower kernel germinates first. Seed dormancy of wild cereals, therefore, poses no limitation to cultivation as about 50% of the sown seeds will germinate and the empty space between the resultant plants will be filled by the tillering typical of the grasses. Thus, selection of seed-dormancy-free types could be automatically obtained by sowing-harvesting cycles. In pulses, on the other hand, the elimination of the seed-dormancy mechanism was apparently a prerequisite for cultivation.

Selection of non-brittle spikes marked a major event in cereal domestication; its impact on Neolithic farming has been widely discussed (Harlan et al. 1973; Kislev 1985). In contrast, pod indehiscence was far less important in pulse domestication. This conclusion is also supported by the fact that some degree of seed loss by shattering is still typical of landraces and endemic varieties in the Middle East and central Asia.

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Book Review

Mistel [mistletoe]—Arzneipflanze, Brauchtum, Kunsmotiv im Jugendstil. Hans Becker and Helga Schmoll-Eisenwerth. Wissenschaftliche Verlagsgesellschaft mbH, Birkenwaldstrasse 44, 7000 Stuttgart, Germany. 1986. 132 pp. with color. $26.36 (paper).

Professor Becker of Heidelberg, and Dr. Schmoll-Eisenwerth of Munich, deserve praise and gratitude for creating a work of scientific importance, high physical quality, and irresistible beauty. Their book is a celebration of European mistletoe (*Viscum album* L.). The text (in German) describes the plant and its various medicinal uses, historical and modern, its chemistry, the extracts currently applied in cancer therapy, their cytostatic and cytotoxic activity, their effects on the immune system, and clinical tests—all supported by a substantial bibliography.

There follow splendid reproductions of paintings of mistletoe and a mistletoe-gatherer, and 29 other (mostly full-page) color plates showing handsome and precious vases, jars, pitchers, compotes, plates, jewelry, and sundry objets d'art decorated with artistic representations of mistletoe. Next are chapters on mistletoe in mythology, folklore, and graphic arts illustrated with half-tones which show elegant combs, brushes, mirrors, sewing kit tools, miniature picture frames, flasks, napkin rings, silver tableware, boxes, pendants and other pieces of adornment, greeting cards, and even cartoons, all with the mistletoe motif, and explained in an lengthy list of annotations. Lastly there are indexes, Part 1 and Part 2.

The book, apart from its medical aspects, is a revelation of human fascination with mistletoe and a pictorial delight with or without a knowledge of German or the aid of a translator.

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