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Six seasons of wild pea harvest in Israel: bearing on Near Eastern plant domestication

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ABSTRACT

Harvest experiments of wild crop relatives are essential for our understanding of the biology of wild plants embodied in the economy of ancient forager communities. Most of the previous experimental harvest reports spanned a single season and therefore are unable to address questions concerning long-term yield potential. Herein we report on six consecutive harvest seasons taking place at four sites in Israel that harbour wild pea populations: three typical *Pisum fulvum* sites and one typical *Pisum elatius* site. Three out of the four sites showed no indication of a decline in grain yield as a result of repeated harvest and the removal of a considerable portion of mature seeds. Site-specific factors seem to have a strong influence on the grain yield as no seasonal yield similarity was observed between adjacent and ecologically similar sites harbouring the same wild pea taxon. The erratic year-to-year wild pea yield we observed calls for a reassessment of the presumed role of grain legume species in Near Eastern hunter–gatherers' diet. Combined with published data on cultivation of wild pea, our results are inconsistent with models suggesting protracted domestication of Near Eastern grain legumes or with the preliminary attempts to apply Niche Construction Theory to the study of plant domestication in the Near East.

1. Introduction

Ancient plant–human liaison is assumed to have relied heavily on the biological features of the wild species involved (e.g., Harlan, 1992; Abbo et al., 2009). Consequently, systematic experimental harvest studies in natural ecosystems of wild taxa that were adopted as crop plants (and their close relatives) during the Neolithic Revolution contribute to our understanding of the cultural and biological processes underlying plant domestication (e.g., Harlan, 1967; Ladizinsky, 1975; Kislev et al., 2004; Abbo et al., 2008a,b) as do population structure and yield potential of wild crop relatives (e.g., Abbo et al., 2008a,b; Ladizinsky, 1975, 1987).

Rindos (1980) suggested that the interdependence between Man and crops (namely, an economy based on food production by means of domesticated plants) has developed along co-evolutionary trajectories similar to those that characterize other natural phenomena of mutualism between genetically unrelated organisms such as ants and fungi (see Purugganan and Fuller, 2011). A recent development along this line of thought is the application of Niche Construction Theory to the study of plant domestication (e.g., Smith, 2007, 2011; Laland and O'Brien, 2010). This approach views plant domestication as the end result of a long co-evolutionary continuum representing the interaction between humans and their target plants. Starting with mere foraging, progressing through increasing levels of intervention throughout which human energy was invested in the wild ecosystem to promote growth of desired species, the process eventually culminated in the cultivation of wild stocks, which is often seen as the critical stage on the brink of plant domestication (e.g., Harris, 1989; for alternative views see review by Abbo et al., 2012).

Domesticated plants differ from their wild progenitors in a number of morphological traits mostly concerning the growth habit, the size and colouration of the economically important (often edible) organs, and features associated with seeds dispersal mode and germination (e.g., Harlan, 1992; Ladizinsky, 1998). The 'Domestication Syndrome' (Hammer, 1984) is a collective term, often used, to denote these morphological differences between cultigens and their wild progenitors. In this context, it is important

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to note that under the abovementioned perpetual human interaction with wild ecosystems (*sensu* Harris, 1989; Smith, 2007, 2011), which may have sometimes, included working the soil, weeding, and other field operations, that cultivated plant populations are thought to have accumulated random mutations that confer better adaptation (the domestication syndrome traits) to the new human-made ecosystem (Harlan et al., 1973; Heiser, 1988; Zohary, 2004). A scenario of automatic selection in human made ecosystems (i.e., cultivated fields) leading to the dominance of domesticated morphotypes in the managed plant community (e.g., Harlan et al., 1973; Zohary, 2004) may seem plausible for cereals. However, it is difficult to consider the domestication of Near Eastern grain legumes as a result of such long-term cultivation, due to their typically strong *wild type* seed dormancy that prevents appropriate seedling emergence and consequently results in no net economic gain (Ladizinsky, 1985; Abbo et al., 2011a).

Hunter–gatherers throughout the world have developed a range of foraging strategies to ensure the sustainability of their food resources (e.g., Kelly, 1995). These foraging patterns include, but are not limited to, seasonal and or year-to-year mobility across the terrain, techniques that may allow for the recovery of wild plant populations that are left un-harvested. Such a strategy is useful only as long as each community has access to sufficiently productive foraging grounds free of competition by neighbouring foraging groups. If human population density increased above a certain threshold, or when sedentism became a cultural and social option, human foraging pressure exerted on wild populations of food plants is likely to have increased in the home range of the respective human communities, or beyond. Such assumed pressures (of demographic growth and sedentism) combined with the onset of a dry-cold climatic regime in the last millennium of the Natufian (Younger Dryas), played a major role in the formulation of various models aiming to explain the origin of agriculture (e.g., Bar-Yosef, 1998). An early model, “Post-Pleistocene Adaptations” by Binford (1968) is often termed *the marginal zone theory*. According to Binford’s model, sedentism and demographic growth in newly available post-Pleistocene environments resulted in a partial (budding-off) migration from these areas to marginal zones, that is, the less productive, semi-arid Levantine steppe. According to the model, the lower abundance of food plants available at these marginal zones may have caused the migrating populations to attempt growing food plants familiar from their former, more humid, homeland that was part of the oak-pistachio woodland belt of the Near East. The supposed demographic growth and resultant increased competition over food resources is likely to have been the result of two major determinants: population size and its demand for foods and the extent of productivity of targeted wild plants. It is thus important to understand the productivity pattern of Near Eastern wild food plant populations. This requires deep insight into the biology of both cereals and legumes, the two major plant groups that gave rise to the major grain crops of the Neolithic Near East (Weiss and Zohary, 2011; Zohary et al., 2012).

A number of biological features fundamentally distinguish between these two plant groups (Abbo et al., 2009). The most important difference between Near Eastern legumes and cereals (both wild and domesticated) concerns the indeterminate growth habit of legumes, in which flowers develop from lateral meristems found along the stems, compared to the determinate growth habit of cereals, in which only apical terminal meristems form spikes. This seemingly technical difference is of great importance because it results in a relatively uniform, synchronous spike ripening in cereal stands, which bears on harvesting prospects. The relatively synchronous ripening of cereals allowed the hunter–gatherer populations to harvest a considerable portion of the cereal yield at any one location in a single visit, whereas only a small fraction of the gradually ripening legume yield may be harvested at any one time (see Abbo et al., 2009: Fig. 1). With legumes, foraging when only the first pods are mature leaves the upper stem nodes unexploited because they still carry flowers and immature pods. Alternatively, timing the harvest towards the end of the ripening season could easily result in the loss of the majority of the seeds from the early formed pods that have dehisced upon maturity (Abbo et al., 2009). Another important difference between cereals and legumes pertains to the degree of their seed dormancy. In the cereals, about 50% of the seeds will germinate following the start of the next rainy season. In wild legumes, however, seed dormancy, mediated by hard (water impermeable) seed coats, is in the range of 90%, allowing only a meagre 10% of the seeds to germinate with the autumn rains (Harlan et al., 1973; Werker et al., 1979; Ladizinsky, 1985, 1987; Abbo et al., 2009: Fig. 1F–H, 2011a).

In addition to these two differences, Near Eastern cereals exhibit better tillering capacity and stronger competitiveness in dense plant populations as compared to the same traits in Near Eastern legumes (Abbo et al., 2009). While this implies that wild legumes and cereals would respond differently to repeated human foraging pressure, no data is currently available regarding the response of Near Eastern wild legume populations to repeated seasonal foraging. In an attempt to compile data on experimental harvest of Near Eastern crop wild relatives, we have noted that with the exception of the *Cicer judaicum* and *Lens* sp. collected by Abbo et al. (2008b), all the above-mentioned experimental harvest studies in the Near East were single season studies. It is thus very difficult to draw any conclusions regarding the role of such wild resources in the long-term economy of hunter–gatherers. It is therefore important to find out the year-to-year potential of wild legume populations as a source of staple grains for foragers as well as the degree to which this potential is influenced by repeated foraging pressure. To answer these questions, this work has targeted wild pea populations harvested for six consecutive seasons.

2. Materials and methods

2.1. The wild Pisum species and their habitats

Wild peas were harvested at four sites located in the Mediterranean district of Israel: Etziyona junction, Machsiya, Latrun, and Wadi Amud (for site details see Table 1 of Abbo et al., 2008a). The locations of these four sites are depicted in Fig. 1, and note the relative proximity of the Etziyona and Machsiya sites. Sites were selected being as free as possible from recent over-grazing and protected from current human interference.

The two wild pea species (*Pisum fulvum* and *Pisum elatius*) targeted in our experimental harvests are half shade plants (Zohary, 1972). In the Levant, these two wild taxa usually accompany perennial, often spiny, shrubs (e.g., *Rhamnus lycioides* L. and *Ziziphus* sp.) found at the edges of forest clearings (Fig. 2). *P. fulvum* is a typical element of the Levantine oak pistachio woodland while the distribution of *P. elatius* is restricted mostly to moist creeks and the northern high rainfall zone in the Mediterranean district of Israel. An aerial-photo of a typical *P. fulvum* habitat at the collection site of Machsiya (31° 44′ 41″ N; 35° 01′ 40″ E) is provided in Fig. 3, and a general ground view of the site is given in Fig. 4. The specific niches where *P. fulvum* plants were encountered during the study years are marked by a yellow line (Fig. 3). The spatial pattern of the wild pea plants at Machsiya resembles a linear pattern, mostly demarking the border between the wide and low evergreen *Pistacia lentiscus* shrubs and the surrounding areas dominated by herbaceous plants (Figs. 3 and 4). It is interesting to note that at the site of Wadi Amud, *P. elatius* also has a linear distribution along both sides