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Experimental growing of wild pea in Israel and its bearing on Near Eastern plant domestication

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• *Background and Aims* The wild progenitors of the Near Eastern legumes have low germination rates mediated by hardseededness. Hence it was argued that cultivation of these wild legumes would probably result in no yield gain. Based on the meagre natural yield of wild lentil and its poor germination, it was suggested that wild Near Eastern grain legumes were unlikely to have been adopted for cultivation unless freely germinating types were available for the incipient farmers. Unlike wild cereals, data from experimental cultivation of wild legumes are lacking.
• *Methods* Replicated nurseries of wild pea (*Pisum elatius*, *P. humile* and *P. fulvum*) were sown during 2007–2010 in the Mediterranean district of Israel. To assess the effect of hardseededness on the yield potential, seeds of the wild species were either subjected to scarification (to ensure germination) or left intact, and compared with domesticated controls.
• *Key Results* Sowing intact wild pea seeds mostly resulted in net yield loss due to poor establishment caused by wild-type low germination rates, while ensuring crop establishment by scarification resulted in net, although modest, yield gain, despite considerable losses due to pod dehiscence. Harvest efficiency of the wild pea plots was significantly higher (2–5 kg seeds h^{-1}) compared with foraging efficiency in wild pea populations (ranging from a few grams to 0·6 kg h^{-1}).
• *Conclusions* Germination and yield data from ‘cultivation’ of wild pea suggest that Near Eastern legumes are unlikely to have been domesticated via a protracted process. Put differently, the agronomic implications of the hardseededness of wild legumes are incompatible with a millennia-long scenario of unconscious selection processes leading to ‘full’ domestication. This is because net yield loss in cultivation attempts is most likely to have resulted in abandonment of the respective species within a short time frame, rather than perpetual unprofitable cultivation for several centuries or millennia.

Key words: Legume domestication, pre-domestication cultivation, protracted vs. contracted plant domestication, wild pea, *Pisum elatius*, *P. humile*, *P. fulvum*.

INTRODUCTION

The first grain crops of the Neolithic Near East included three cereals, diploid einkorn wheat (*Triticum monococcum*), tetraploid emmer wheat (*T. turgidum*) and barley (*Hordeum vulgare*), and four grain legumes (pulses), lentil (*Lens culinaris*), pea (*Pisum sativum*), chickpea (*Cicer arietinum*) and bitter vetch (*Vicia ervilia*.) (Zohary and Hopf, 2000). Both wild progenitors and domesticated forms of these two crop groups (cereals and legumes) differ in many aspects (Butler, 1992, 2009; Abbo *et al.*, 2009). The above-mentioned cereals are tall stature plants with aggressive, competitive and determinate growth, approx. 50 % seed dormancy (wild forms) and 0·5–10 % cross-pollination; while the legumes are mostly weak competitors, low stature plants (except pea), have indeterminate growth and mostly cleistogamous flowers with a very low rate of cross-pollination (Abbo *et al.*, 2009). These profound biological differences required a differential treatment for each of the wild progenitors during the early manipulation of wild plants, which in turn resulted in successful domestication (Abbo *et al.*, 2009). Accordingly, the special attention and selection pressures applied to the different taxa, and crop-specific husbandry regimes under domestication resulted in different evolutionary trajectories, as indeed is expressed in the different adaptation profiles of the different crops in present-day agriculture (Abbo *et al.*, 2003, 2009; Butler, 2009).

One of the major differences between the wild progenitors of Near Eastern grain legumes and cereals concerns the low germination rate imposed by the hard seed coat of these legumes (Werker *et al.*, 1979; Ladizinsky, 1985; Abbo *et al.*, 2009, and references therein). Hence, sowing wild wheat or barley with their approx. 50 % germination and profuse tillering may easily produce an agronomic-like stand capable of competing with weeds, with dozens (often more) of spikes per square metre, as can often be seen in undisturbed wild barley or emmer populations (Noy-Meir

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et al., 1989; Noy-Meir, 1990; Zohary and Brick, 1961). We are unaware of published records on experimental cultivation of wild Near Eastern grain legumes, but, based on their published low (5–20 %) germination rates (e.g. Ladizinsky, 1985, 1987), sowing wild pea, lentil, bitter vetch or chickpea is expected to result in poor stands likely to be overtaken by aggressive competitors.

Based on the poor productivity of wild lentil (*L. orientalis*) in its wild habitats and its strong seed dormancy (approx. 90 %), Ladizinsky (1987, 1993) suggested that wild lentils were unlikely to have been adopted as candidates for cultivation unless a freely germinating ('domesticated') type was available/known to the Neolithic incipient farmers. This unorthodox contention of Ladizinsky (1987, 1989, 1993), which can be summarized briefly into 'pulse domestication before cultivation' (the title of Ladizinsky's 1987 article), attracted severe criticism stressing the relative importance of the breakdown of the wild seed dispersal mode over free germination in pulse domestication (Zohary, 1989; Blumler, 1991). The experimental harvest of wild lentils by Abbo *et al.* (2008*a*) provided strong support for Ladizinsky's (1987, 1989, 1993) arguments regarding the dietary role of lentil prior to their domestication; however, in the absence of data from experimental cultivation of Near Eastern legumes the debate is likely to remain unresolved. The Ladizinsky–Zohary–Blumler debate focused mainly on lentils; however, it should be borne in mind that Ladizinsky has used the biology of wild and domesticated lentil to put forward a general model for Near Eastern pulse domestication (Ladizinsky, 1987).

This study was performed in an attempt to broaden the above discussion, and in the context of our work on the domestication of Near Eastern grain legumes (e.g. Abbo *et al.*, 2009). Our aims were 2-fold: first, to compare the potential of wild pea populations as a food source (Abbo *et al.*, 2008*b*) with the yield potential of 'cultivated' wild pea, we have sown wild pea nurseries during the 2007–2010 growing seasons in Israel. Secondly, using domesticated pea plots as a reference, we used these experimental wild pea nurseries to evaluate the role of the free germination trait in pea domestication. The grain yield pattern of the wild pea plots is discussed with special emphasis on the classical domestication syndrome traits, free germination and pod indehiscence (e.g. Zohary 1989). In light of the above, we conclude by contrasting our experimental data against the recently suggested 'protracted domestication model' (*sensu* Allaby *et al.*, 2008).

MATERIALS AND METHODS

Plant material

As seed sources for the 'cultivation' experiments we used seeds harvested from wild populations of three wild *Pisum* species, all native to Israel (Abbo *et al.*, 2008*b*). These are *P. fulvum* Sibth & Sm., *Pisum elatius* M. Bieb. and *P. humile* Boiss. & Noë considered as the wild progenitors of domesticated pea *P. sativum* (Ben-Ze'ev and Zohary, 1973). In this paper we follow the taxonomy of Ben-Ze'ev and Zohary (1973); however, some pea scientists recognize only two species in the genus *Pisum*, namely *P. fulvum* and *P. sativum*, and grant the taxa which are closely related to the cultigen (*P. elatius*, *P. humile*) a sub-specific rank (e.g. Maxted and Ambrose, 2000).

Initial seed increase of *P. fulvum* and *P. elatius* took place in 2006 using seed mixtures from different wild populations of each taxon. Seed increase of *P. humile* took place during 2007. As a reference, we used domesticated field pea (*P. sativum*) cv. Dunn donated by the 'Hazera Genetics' seed company, Israel.

'Cultivation' nurseries

Seed scarification (to allow free germination) was done by pinching individual seeds with tweezers to remove a small part of the water-impermeable seed coat.

The nurseries were sown in several sites within the Mediterranean district of Israel where the mean annual precipitation is close to 400 mm of rain, which mostly occurs between October and April. The nurseries were set within dryland legume fields (either common vetch or clovers). Details of the experimental sites, including their exact location, soil type and rainfall are given in Table 1.

We used a randomized block design with four replicates, with 2 × 2 m plots and 1 m lanes separating adjacent plots. For each of the wild species two treatments were included in each block: intact seeds and scarified seeds, both at a rate of 100 seeds m^{-2}. In 2007 and 2010, the domesticated cv. Dunn reference field pea was included using intact seeds only. In the 2008 and 2009 nurseries, the domesticated reference cultivar was included in both seed treatments (intact and scarified) in a balanced experimental design. Weeds were removed manually several times during the growing season.

The nurseries were sown between mid-December and mid-January of each growing season to allow removal of the first germinating volunteers from previous crops and weeds after the first autumn rains. The seeds were scattered along shallow furrows (approx. 0·25 m row spacing), which were covered using rakes to minimize seed predation by birds and rodents. In the case of a long interval between rain events, supplementary irrigation was applied, but the total rain plus irrigation never exceeded 450 mm in any of the sites in all years. Due to the repeated drought in 2007–2010 and early cessation of the rainy seasons, several nurseries were abandoned since the relatively late flowering species *P. elatius* and *P. humile* failed to set any pods, and at times even dried out prior to flowering.

Upon physiological maturity (partial pod drying) of each species the plants were harvested by hand pulling and placed in paper bags. The harvested material was placed in forced-air drying ovens at 39 °C for 3–4 d. After drying, the plant material was manually separated into straw and seeds, and both fractions were weighed.

During the harvest of the 2007 nurseries, we measured the time (min) required to harvest all pea plants from each plot at the site. These values were used for comparison with the published data of harvest efficiency of naturally occurring wild pea (Abbo *et al.*, 2008*b*).

TABLE 1. *Geographic and environmental details of the wild pea experimental nurseries during the years of the study*

Site	Longitude (°E)	Latitude (°N)	Geographic region	Soil type	Altitude (m a.s.l.)	Average annual rainfall (mm)	Rainfall during the study years: total, date; amount of last effective rain event (mm)	Mature grains harvested (year: Yes/No)
Gadot	035°37′	33°01′	Hule Valley	Basaltic vertisol	100	450	2007: 416, April; 30 mm*	2007: No
Metzer	033°04′	32°27′	Samaria foothills	Alluvial vertisol	80	580	2008: 485, February 15; 35 mm	2008: No
							2009: 530, March 14; 25 mm	2009: No
Bet-Guvrin	034°52′	31°36′	Judean foothills	Alluvial vertisol	260	370‡	2007: 458, March 16; 31 mm	2007: Yes
							2008: 290, February 20; 44 mm	2008: Yes
							2009: 325, March 23; 40 mm	2009: No
							2010: 311, March 26; 25 mm†	2010: No
Cheletz	034°39′	31°36′	Coastal plain	Alluvial vertisol	100	470	2008: 317, February 19; 48 mm	2008: No
Kokhav	034°41′	31°38′	Coastal plain	Alluvial vertisol	100	470	2007: 395, February 27; 27 mm	2007: Yes
Lakhish	034°49′	31°33′	Judean foothills	Alluvial vertisol	200	340‡	2010: 357, March 26; 43 mm†	2010: No

* After 40 mm only in March.
† After 30 d with no rainfall.
‡ Average of last 10 years.

TABLE 2. *Mean emergence rate at the three pea nurseries in 2007*

(a) Site		
	Emergence (%)	s.d.
Gadot	64·1	37·8
Bet-Guvrin	59·1	39·2
Kokhav	48·8	32·9
(b) Treatments across sites		
	Mean germination rate (%)	
Domesticated, intact	89·1[a]	
P. elatius, scarified	83·9[ab]	
P. fulvum, scarified	76·3[b]	
P. fulvum, intact	35·9[c]	
P. elatius, intact	1·3[d]	

Mean values across the three species (domesticated *P. sativum* cv. Dunn, wild *P. fulvum* and wild *P. elatius*) and two seed treatments. Mean emergence rate (%) of intact domesticated pea compared with intact and scarified wild *P. fulvum* and wild *P. elatius* seeds across the three pea nurseries. The statistical analysis was performed on the transformed values. Means followed by the same letter do not differ according to the Tukey HSD test ($P < 0.05$).

TABLE 3. *Mean grain yield of intact domesticated pea compared with intact and scarified wild* P. fulvum *and wild* P. elatius *seeds across the Bet-Guvrin and Kokhav pea nurseries in 2007*

Treatment	Mean grain yield (g per 4 m^2)
Domesticated, intact	597·6[a]
P. fulvum, scarified	136·9[b]
P. elatius, scarified	82·2b[c]
P. fulvum, intact	15·2[c]
P. elatius, intact	0·7[c]

Means followed by the same letter do not differ according to the Tukey HSD test ($P < 0·05$). Note that in each wild pea plot 40 g of seeds were sown.

RESULTS

2007 season

Mean germination rate (across seed treatments) was quite similar (48·9–64·1 %) in the three sites, with somewhat lower values at Kokhav (Table 2). The scarification treatment had a marked effect on the germination rate of the wild pea seeds in the three experimental sites (Table 2). We were not interested in examining the scarification effect on domesticated pea germination, and therefore did not include a treatment combining domesticated–scarified seeds, so only intact domesticated pea seeds were sown to be contrasted with the response of the wild species. Consequently we used a two-way analysis of variance (ANOVA) model with site, species–scarification and site × species–scarification interaction term, rather than three-way ANOVA (site, species, seed treatment and their interactions). The results of the Tukey HSD test are depicted in Table 2, and demonstrate the dramatic qualitative difference between domesticated pea and the two tested wild species (*P. elatius* and *P. fulvum*). Scarified wild pea seeds germinate readily with values very similar to those of domesticated pea, while intact wild pea seeds had low germination rates (Table 2). The intermediate values of the intact *P. fulvum* seeds most probably resulted from the use of 2- and 3-year-old seeds, harvested in previous seasons in wild populations.

Due to the drought, the ANOVA of the grain yield results included the Kokhav and Bet-Guvrin nurseries only. The only factor with a significant effect was the ‘species–scarification’. The mean grain yield values of the domesticated species and the two wild species (*P. elatius* and *P. fulvum*) are given in Table 3. As with the germination values, the grain yield values can be divided qualitatively into two groups; domesticated + wild–scarified vs. wild–intact seed. This is because, without exception, sowing intact wild pea seeds resulted in net grain yield loss, while sowing scarified wild seeds always resulted in net grain yield gain.

2008 and 2009 seasons

In these two years a treatment of scarified domesticated pea seeds was included, and therefore the results were analysed in

TABLE 4. *Mean emergence rate of intact and scarified domesticated and wild pea (*P. fulvum*,* P. elatius *and* P. humile*) seeds across the six pea nurseries in 2008 and 2009*

Treatment	Mean germination rate (%)
Domesticated, scarified	81·4[a]
Domesticated, intact	78·7[a]
P. elatius, scarified	77·4a
P. fulvum, scarified	73·7[a]
P. humile, scarified	71·0[a]
P. fulvum, intact	19·1[b]
P. elatius, intact	15·6[b]
P. humile, intact	8·9[b]

The statistical analysis was performed on the transformed values. Means followed by the same letter do not differ according to the Tukey HSD test ($P < 0·05$).

TABLE 5. *Mean grain yield of intact and scarified domesticated and wild pea (*P. fulvum*,* P. elatius *and* P. humile*) seeds in the Bet-Guvrin pea nursery in 2008*

Treatment	Mean grain yield (g per 4 m^2)
Domesticated, intact	724·3[a]
Domesticated, scarified	614·0[a]
P. humile, scarified	280·4[b]
P. fulvum, scarified	231·6[b]
P. elatius, scarified	170·4[bc]
P. fulvum, intact	66·5[cd]
P. elatius, intact	48·4[cd]
P. humile, intact	23·1[d]

Means followed by the same letter do not differ according to the Tukey HSD test ($P < 0·05$). Note that in each wild pea plot 40 g of seeds were sown.

a balanced ANOVA model, which included the species, the scarification treatments, the site, the year and all respective interactions. The year effect on the germination rate was not significant and was later removed from the model. The mean germination rates in the different combinations of pea species and seed scarification are given in Table 4, and can be divided into two main groups of domesticated + wild–scarified vs. wild–intact.

Seeds from all three wild pea species were harvested only in the Bet-Guvrin 2008 nursery. In all other sites the plants suffered from early termination of the rainy season, resulting in collapse of most plots of the relatively late flowering *P. elatius* and *P. humile* wild pea species. The mean grain yield values of the domesticated species and the three wild species are given in Table 5. As with the germination values, the grain yield values can be divided qualitatively into two groups; domesticated + wild–scarified vs. wild–intact seed. Sowing of intact wild *P. humile* seeds resulted in net grain yield loss, and sowing intact *P. elatius* and *P. fulvum* seeds resulted in meagre grain yield gain; while sowing scarified seeds from all three wild species always resulted in a 4- to 7-fold grain yield return.

2010 season

The mean germination rates of the three wild *P. elatius* genotypes and the domesticated control cultivar in the two experimental sites are given in Table 6. As in the previous experiments, the germination values could be grouped into two categories; one comprising plots sown to domesticated (intact) + scarified wild pea, and a second category of plots sown to intact wild pea. The mean germination rate of the domesticated pea and the scarified wild pea ranged between 85 and 97 %, while in plots sown to intact wild pea seeds the mean germination rate was between 2·5 and 7 %. Due to an early cessation of the rainy season we had to abandon the two nurseries since most of the plots had dried out prior to pod filling.

TABLE 6. *Mean emergence rate of intact and scarified wild pea (*P. elatius*) seeds across the two pea nurseries in 2010*

Treatment	Mean germination rate (%)
Domesticated, intact	85·6[a]
P. elatius (Wadi Amud), scarified	97·2[Aa]
P. elatius (Wadi Kziv 1), scarified	77·1[Aa]
P. elatius (Wadi Kziv 2), scarified	92·7[Aa]
P. elatius (Wadi Amud), intact	3·5[Bb]
P. elatius (Wadi Kziv 1), intact	2·6[Bb]
P. elatius (Wadi Kziv 2), intact	7·3[Bb]

The statistical analysis was performed on the transformed values: Upper-case letters are used to compare the mean germination rate among the three wild genotypes; lower-case letters are used for comparisons that include the intact domesticated pea control cultivar. Values followed by the same letter do not differ according to the Tukey HSD test ($P < 0·05$).

DISCUSSION

Grain yield and harvest efficiency of wild pea

The mean grain weight of the three wild pea species is approx. 0·1 g seed^{-1}. Therefore, to sow 4 m^2 plots to 100 seeds m^{-2} we had to use approx. 40 g. In all our cultivation experiments, the germination rate of the intact wild seeds was low (mostly <20 %), resulting in most cases in no meaningful grain yield return beyond the invested seeds (Tables 3 and 5).

We also measured the time required to harvest each of the plots of the Bet-Guvrin nursery in 2007. Accordingly, it was estimated that in plots sown to scarified *P. fulvum* seeds, one could harvest, within an hour, plant material that, after threshing (which requires additional time investment), would yield 2–5 kg of clean seeds. For 'cultivated' *P. elatius* the harvest efficiency was estimated to be between 0·4 and 2·8 kg h^{-1}. These values are higher compared with those recorded in our wild pea foraging experiments in wild populations, which mostly were <0·2 kg h^{-1} (Abbo *et al.*, 2008*b*). It should be noted that our grain yield and harvest efficiency values were obtained from plants with a wild-type dehiscent pod genotype. In indeterminate grain legumes it is impossible to avoid some yield losses during harvest because as the plants progress to full maturity the ripened pods from the lower internodes usually shatter and release their seeds (see Abbo *et al.*, 2009). Likewise, in our nurseries, in many plots, considerable numbers of seeds were seen on the ground on the day of harvest and were not collected. The higher harvest efficiency of 'cultivated' wild pea (given free germination) may be considered as part of the economic incentive to embark on legume farming. Stated differently, provided that freely germinating types are available, the cultivation of wild peas (with a wild-type seed dispersal mode) is by far more efficient than foraging in wild pea populations.

The profitable 'cultivation' of wild pea with wild-type dehiscent pods, after ensuring germination by scarification, may help to resolve the Ladizinsky (1987)–Zohary (1989) debate regarding the relative importance of free germination vs. pod indehiscence in pulse domestication. In our view, there is no doubt that pod indehiscence is very important in preventing seed loss at full maturity. However, our yield data suggest that the free germination trait was a more important criterion for the adoption of a wild pea (and possibly lentil and chickpea as well) than their seed dispersal mode. Our results therefore reaffirm Ladizinsky's (1993) contention that it is highly unlikely that Neolithic farmers would have made the effort to domesticate lentil (or another wild Near Eastern legume) without knowing of freely germinating types that occur naturally (see Abbo *et al.*, 2011) or that were already at hand.

The data in Table 1 suggest that the total annual rainfall was not the only limiting factor. No less important were the actual germination date, the seasonal rain distribution, pest infestation and diseases, and, most importantly, the occurrence of hot spells during the early spring months (data not shown). Such events caused terminal drought and prevented proper reproduction mostly in the late flowering taxa *P. humile* and *P. elatius*. The frequent crop failure events may provide an important clue concerning the geographic origin of Near Eastern agriculture. Although we claim that genetic, biogeographic and archaeological data lend strong support to the idea of a 'core area' in south-eastern Turkey (*sensu* Lev-Yadun *et al.*, 2000; Abbo *et al.*, 2010), some students of the subject support a diffused origin for Near Eastern farming across the Fertile Crescent (e.g. Brown *et al.*, 2009), and many stress the role of the southern Levant (e.g. Kislev, 2002; Weiss *et al.*, 2006; Feldman and Kislev, 2007). The results of our experimental wild pea cultivation make it hard to assume that pea domestication resulted from intensification attempts in marginal zones in general (and see Binford, 1968), and in the southern Levant in particular. Otherwise, we find it hard to understand why *P. fulvum* was not adopted for domestication (rather than *P. humile*), given its earlier flowering habit which gives it better adaptability to the southern Levant (attested from its natural distribution range; Ben-Ze'ev and Zohary 1973) and the consequent higher prospects for escape from drought.

Domestication in the slow lane?

Domestication by way of long-term cultivation of wild plants is a common theme in the recent literature on the origins of agriculture (e.g. Kislev, 2002; Tanno and Willcox, 2006; Fuller, 2007; Allaby, 2008; Allaby *et al.*, 2008; Brown *et al.*, 2009; Fuller *et al.*, 2009, 2010; Fuller and Allaby, 2010; Purugganan and Fuller, 2010). These authors see domesticated crops as the result of a protracted evolutionary process (at times millennia long), which was driven by selection pressures exerted by the incipient 'cultivators' (e.g. Kislev, 2002; Zohary, 2004; Fuller, 2007; Purugganan and Fuller, 2010). In wheat and barley, archaeological spike remains can be used to trace the appearance of non-brittle (domesticated) types, and quantification of domesticated spike remains relative to the total archaeobotanical finds was used to determine the time frame required for the domesticated genotypes to dominate the population (e.g. Tanno and Willcox, 2006; Purugganan and Fuller, 2010). Unlike the cereals, Near Eastern grain legume remains have no archaeologically visible morphological marker for domestication (Butler, 2009), but some authors try to use the gradual change in seed size throughout the presumed domestication period (as deduced for the cereals) to quantify the change in population structure during the relevant period (e.g. Purugganan and Fuller, 2010).

It could be argued that the incipient 'cultivators' have used their immense knowledge of their surrounding biota (e.g. Levi-Strauss, 1962; see Abbo *et al.*, 2011) to scarify the wild pea seeds (between stone slabs, ageing for >2 years, etc.) in order to ensure proper crop establishment and thereby secure the grain yield. However, under such circumstances it is even more difficult to understand how a spontaneous free-germinating mutant could have been identified, isolated and selectively propagated. This is because the uniform germination of the scarified wild seed stocks does not enable the wild-type and the freely germinating genotypes to be distinguished (as in our own wild pea nurseries).

In conclusion, contrary to the claims regarding a protracted domestication process, our yield data from wild pea 'cultivation' experiments suggest that pea (and most probably lentil and chickpea) is unlikely to have been domesticated via a protracted process. Stated differently, the agronomic implications of wild legume hardseededness are incompatible with a scenario of a protracted, unconscious selection process. This is because net yield loss in cultivation attempts was most likely to have resulted in abandonment of the respective species within a short time frame, rather than perpetual uneconomic activity for several centuries or millennia.

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