

RESEARCH PAPER

Did greater burial depth increase the seed size of domesticated legumes?

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Abstract

The independent domestication of crop plants in several regions of the world formed the basis of human civilizations, and attracts considerable interest from archaeologists and biologists. Selection under cultivation led to a suite of domestication traits which distinguish crops from their wild progenitors, including larger seeds in most seed crops. This selection may be classified as ‘conscious’ or ‘unconscious’ selection according to whether humans were aware of the changes that they were driving. The hypothesis that human cultivation buried seeds deeper than natural dispersal, exerting unconscious selection favouring larger seeds with greater reserves, was tested. Using a comparative approach, accessions of eight grain legumes, originating from independent domestication centres across several continents, were sampled. Seeds were planted at different depths in a controlled environment, and seedling emergence scored for 5 weeks after sowing. Domestication in all species was associated with increased seed mass. In three species, greater mass was not correlated with increased ability to emerge from depth. In five species, emergence depth did correlate with mass, suggesting that selection during domestication may have acted on emergence depth. However, domestication only had a significant effect in two of these species (lentil and mung bean), and the increase in depth was no more than predicted by a cube-root allometric relationship with seed mass. The results do not support the hypothesis that burial under cultivation was a general selection mechanism for increased seed mass during the domestication of grain legumes, but it may have acted in particular species or regions.

Key words: Crop domestication, emergence depth, origins of agriculture, seed burial, seed size, unconscious selection.

Introduction

The origin of agriculture is one of the most fundamental changes in human history, and it has attracted considerable interest from both archaeologists and biologists. Human societies first began to cultivate wild plants and to manage animal populations around 10 000 years ago in several distinct regions (Gepts, 2004, p. 14; Cohen, 2009). While the Fertile Crescent in Western Asia is the best studied, emerging evidence suggests that agriculture began in China and in Central America soon afterwards (Piperno *et al.*, 2000, 2009; Crawford, 2009), and a number of other areas have been proposed as later independent centres of origin,

including Africa, India, New Guinea, and Eastern North America (Denham *et al.*, 2003; Fuller, 2006; Smith, 2006; D’Andrea *et al.*, 2007). Interactions with humans changed the selection pressures acting on the cultivated plants and managed animal species, and drove relatively rapid evolution on a millennial time scale, leading to the emergence of distinct domestic forms (Purugganan and Fuller, 2011). In many cases, the progenitors of these domestic species still exist in the wild, providing a unique control group that allows examination of the processes leading to domestication.

The domestication syndrome (Hammer, 1984) is a collection of traits that sets domestic races or species apart from their wild progenitors (Harlan *et al.*, 1973; Zohary, 1989; Fuller, 2007; Brown *et al.*, 2009). In plants, this typically includes the loss of dispersal mechanisms, such as shattering ears (in cereals) or indehiscent pods (in grain legumes), as well as increased seed size, reduced seed dormancy, a decrease in the number of tillers, and greater synchrony in their development (in cereals). Although debate continues over whether agriculture began rapidly in a small area, or gradually over a broader area (Abbo *et al.*, 2010; Fuller *et al.*, 2011, 2012; Peleg *et al.*, 2011), there is some evidence that domestication traits did not evolve simultaneously (Tanno and Willcox, 2006; Weiss *et al.*, 2006; Fuller, 2007). For example, archaeobotanical evidence shows that non-shattering forms of barley and einkorn wheat in the Fertile Crescent increased gradually under cultivation from around 9000 BC to around 7000 BC, while the increase in seed size could have taken less than a millennium (Fuller, 2007).

Various possible explanations, which are not mutually exclusive, have been advanced to explain the increase in seed size observed during domestication. These invoke either 'conscious selection' (i.e. involving deliberate selective breeding for a particular trait by the early farmers) or 'unconscious selection', in which selection on the trait is an unintended consequence of the cultivation, crop management, or harvest regime (Darwin, 1875, Chapter 20). For instance, dispersal mechanisms may have been lost under unconscious selection, as seeds remaining on the plant were more likely to be collected and re-sown by early farmers (Hillman and Davies, 1990; Fuller and Allaby, 2009).

One current hypothesis for the increase in seed size focuses on the processes of germination and seedling emergence. It holds that seeds were generally buried deeper by deliberate human planting than by dispersal in a natural environment. The need to emerge from a greater depth in the soil would have selected for seeds with larger reserves (Harlan *et al.*, 1973; Zohary, 2004; Purugganan and Fuller, 2009). In particular, the development of simple animal-pulled ploughs some time after domestication (Lal *et al.*, 2007) has been proposed as an explanation for the late increase in seed size observed in grain legumes in the archaeological record (Fuller, 2007). Archaeological evidence also suggests that early cultivation may have been in small-scale, intensively managed 'gardens', where seeds could have been sown by dibbling, dropping seeds into individually made holes, rather than broadcasting, in which seed is scattered over a tilled plot (Bogaard, 2005; Jones, 2005); the former would be more likely to bury seeds deeper. There is some archaeobotanical evidence supporting the burial hypothesis, primarily from Indian *Vigna* species (mung and urd bean), where the seed size starts to increase approximately contemporaneously with the development of the ard plough (Fuller and Harvey, 2006). Ecological experiments have demonstrated repeatedly that larger seeded species are able to emerge from greater depths (Bond *et al.*, 1999; Benvenuti *et al.*, 2001; Pearson *et al.*, 2002). However, experiments that have compared seeds within species have produced more mixed results (Townsend, 1992; Qiu and Mosjidis, 1993;

Chen and Maun, 1999; Gan *et al.*, 2003; Li *et al.*, 2006). A literature search found a single study comparing wild and domestic forms of a crop species, namely cowpea (*Vigna unguiculata*) (Lush and Wien, 1980). In line with the burial hypothesis, this showed that the larger seeds of the domesticated subspecies were more likely to emerge from 12 cm burial depth, although it tested just one wild and two domesticated accessions.

A comparative experimental approach has been used here to test three predictions of the burial hypothesis in eight legume crop species, domesticated in six regions on different continents. This approach was chosen, rather than focusing on a single crop species or a single region, to look for a general pattern and exceptions to that pattern. Current thinking is that agriculture could have begun independently in all six of these regions (Diamond, 2002; Purugganan and Fuller, 2009), but even the most conservative estimates accept three separate origins, all of which are represented here (Harlan, 1971). The first prediction is that, within crop species, emergence depth is positively correlated with seed size. Secondly, since seed size increases with domestication, domestic accessions should be able to survive deeper burial than wild accessions.

Finally, it is predicted that the effect of domestication on emergence depth exceeds that expected based on seed mass alone. If a selective pressure was favouring seedlings able to emerge from greater depths, various traits besides seed size could respond to that, using the available resources more efficiently to grow upwards to the surface. For instance, seedlings could invest a greater fraction of their reserves in shoot growth, rather than root growth, or produce a proportionately thinner hypocotyl or epicotyl. The effect of such changes would be that crop seedlings are better able to emerge from depth than wild seedlings, even if they had seeds of the same size. However, caution is required in interpreting this, as selection for other factors, such as growth rate, may also have affected these traits.

Materials and methods

Plant material

Eight legume crop species were chosen, representing several geographical centres for the origin of agriculture (Table 1). The sampling strategy was not designed to be exhaustive; for example, only two out of at least five grain legumes domesticated in the Fertile Crescent were sampled. Instead, within the logistic constraints of the experimental set-up, the aim was to cover a broad range of geographical regions, and different sized grains spanning lentil to lima bean. To confirm the expected effect of domestication on seed mass for each species, seed mass data were first collected from the US GRIN/NPGS germplasm database (<http://www.ars-grin.gov/npgs/>), and these were supplemented with the authors' own weight measurements. The data were filtered to include only accessions collected in the region where the crop was domesticated and, where possible, wild and domestic accessions were filtered by species or subspecies as well as the recorded improvement status, to exclude feral (weedy) accessions of domesticated crops.

For seed burial experiments, accessions of each species were obtained from GRIN/NPGS, except for mung bean, which came from the Australian AusPGRIS collection (<http://www2.dpi.qld.gov.au/extra/asp/auspgris/>). As with the larger scale data collection described

Table 1. Legume crop species used

Names follow GRIN taxonomy (USDA, ARS, National Genetic Resources Program).

Origin	Crop	Domestic	Progenitor
Western Asia	Lentil	<i>Lens culinaris</i>	<i>L. culinaris</i> subsp. <i>orientalis</i>
	Pea	<i>Pisum sativum</i>	<i>Pisum sativum</i> ^a
Africa	Cowpea	<i>Vigna unguiculata</i>	<i>V. unguiculata</i> subsp. <i>dekindtiana</i>
South Asia	Mung bean	<i>Vigna radiata</i>	<i>V. radiata</i> var. <i>sublobata</i>
China	Soybean	<i>Glycine max</i>	<i>G. soja</i>
Central/South America	Common bean	<i>Phaseolus vulgaris</i>	<i>P. vulgaris</i> var. <i>aborigineus</i>
	Lima bean	<i>Phaseolus lunatus</i>	<i>Phaseolus lunatus</i>
South America	Peanut	<i>Arachis hypogaea</i>	<i>A. monticola</i>

^a Wild peas includes accessions of *Pisum sativum*, *P. sativum* subsp. *elatius*, *P. sativum* var. *arvense*, and *P. sativum* var. *pumilio*, but in each case had improvement status recorded as 'wild material'.

above, all accessions were originally collected from the region where the crop originated, avoiding feral accessions where possible. If seed mass data were provided by the germplasm database, accessions were chosen to represent as wide a range of seed sizes as possible; otherwise they were chosen at random. Seed listed as landrace accessions was used for the domesticated samples, to minimize the effects of modern commercial crop breeding. For those crop progenitors which do not have a distinct taxonomic name, accessions listed as wild material were used. One lima bean accession was redesignated from landrace to wild after the experiment (based on its dormancy characteristics), so was counted as wild in the analysis.

Emergence depth trial

Accessions were randomly allocated to four blocks, established sequentially, and each containing one wild and one domesticated accession of each crop. Pea (*Pisum sativum*) was excluded from the last two blocks, as data showed that it could consistently emerge from the greatest depths used in the experiment.

Polythene 'layflat' tubing (postpack.co.uk) wrapped with aluminium foil was used to make containers: using 5 cm width tubing (approximate diameter 32 mm) for lentil, pea, cowpea, mung bean, and soybean; and 7.5 cm width tubing (approximate diameter 48 mm) for common bean, lima bean, and peanut, since pilot trials showed that the larger seedlings of these species were constrained by the narrower tubes. While using two different diameters of tubing restricted the possibility of direct comparison between species, the principal aim of the experiment was to compare emergence within species. Tubes were 40 cm long, and were loosely fixed at the bottom to allow drainage.

Up to 20 seeds of each accession were weighed individually, with the exception of wild peanut (*Arachis monticola*), for which only 12 seeds per accession were available. Seeds other than peanuts were scarified with medium grit sandpaper to expose part of the cotyledons, so as to break dormancy. Tubes were packed to a constant density with a soil mix comprising 2:1:1 (by volume) M3 compost (East Riding Horticulture, Yorkshire, UK):Chelford 52 silica sand (Sibelco, Cheshire, UK):perlite (East Riding Horticulture), intended to provide a well-draining medium suitable for a lab screen of seedling traits, and to be easy to pour into narrow tubes. A pilot experiment was done with seeds planted at between 2 cm and 18 cm below the soil surface, to determine the approximate emergence depths of the eight species. The results were used to choose five evenly spaced depths for each species, ranging between 2 cm and 28 cm, such that the deepest planted seedlings would be unlikely to emerge, although pea proved consistently able to emerge from all depths used. Within each accession, seeds were assigned randomly among these depths.

Tubes were watered thoroughly, then placed in a growth room (MTPS 120, Conviron, Winnipeg, Canada), with a 12 h day, 22/20 °C day/night temperature regime, and constant 50% relative humidity. They were subsequently watered at 1 week intervals to maintain a

moist but not waterlogged soil medium, and emergence was recorded daily for 5 weeks. After this period, tubes where a seedling had not emerged were emptied to check for the presence of a seedling; where a seedling was not found, the seed was taken to have not germinated, and the sample was excluded from subsequent analysis.

Statistical analysis

The seed masses of wild and landrace accessions were statistically compared using *t*-tests of log-transformed data, as seed mass data typically follow a log-normal distribution (Leishman *et al.*, 1995; Khazaei *et al.*, 2008). To analyse the emergence data, generalized linear mixed effects models were built using the R package 'lme4', treating each species separately rather than including species as a factor in a combined model. Seedling emergence from the soil surface was the binomial dependent variable (emerged or not), and the independent variables were seed mass and domestication, modelled first separately, then together in an additive model. In each case, accession was included as a non-interacting random effect (allowing accession to interact with depth did not significantly improve model fit). The statistical power of this model was evaluated with simulated data, wherein emergence depth was proportional to the cube-root of seed mass, plus a constant factor for domestication, and a normally distributed error term, with a standard deviation of 4 cm. With data equivalent to a single species (four accessions of each of wild and domestic, five depths, four replicates at each depth), an effect size of 3 cm from domestication was detected as significant in 69% of simulated samples, and an effect size of 4 cm in 91%. With a coefficient of 2 in the seed mass term (selected to bring the simulated emergence depths roughly in line with the results), log seed mass was detected as a significant factor in >95% of samples in both cases.

Survival analysis of the time from sowing to emergence was also performed, using mixed-effects Cox proportional hazard models. Again, accession was included as a random effect, while a separate model was fitted for each crop species. This approach explicitly uses the emergence data, rather than condensing this information to binomial emergence, but it is a more complicated technique, and is normally applied to events which must occur eventually, unlike seedling emergence. This was therefore seen as complementary to the binomial analysis.

Results

Seed mass

In each species, seed mass data collected from germplasm databases and observations confirmed the expected increase in seed mass with domestication (Fig. 1). On average, the

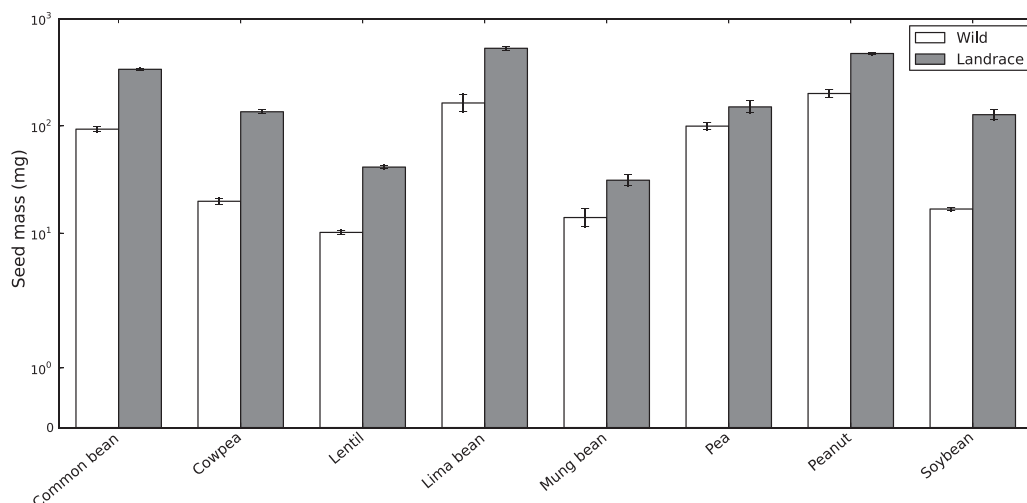


Fig. 1. Seed masses for wild and landrace accessions of the species used in the experiment, plotted on a logarithmic scale. Averages are geometric means of the values for between 6 and 291 accessions, and error bars indicate standard error of the mean.

landrace accessions of a species had seeds that were 3.9 times heavier than the wild accessions; the ratios for individual species are shown in Table 2, ranging from 1.5 for pea to 7.8 for soybean.

Emergence depth

Of 1159 seeds planted, 952 germinated (82%), of which 593 (62%) emerged within 5 weeks (Fig. 2), and subsequent analyses were performed only for those seeds that germinated. The full data set is available as Supplementary data at JXB online. The probability of seeds germinating was affected by depth in only two species (mung bean, $P=3.34 \times 10^{-4}$; cowpea, $P=0.0223$; logistic regression), with seeds of these species less likely to germinate when planted deeper.

In all species besides pea, depth had a highly significant effect on the emergence of seeds that had germinated ($P < 10^{-3}$; Fig. 2). Pea seedlings consistently emerged from even the greatest depth used in the experiment (28 cm), so the models only detected a very weak depth effect. However, emergence was <50% at the greatest depths tested in all

of the other species (Fig. 2). For every accession of species except pea, the generalized linear model fits of logistic curves were therefore used to predict the depth at which 50% of individuals failed to emerge, and these were plotted against seed mass (Fig. 3).

In five of the species (lentil, lima bean, mung bean, cowpea, and pea; approaching significance in soybean), log seed mass was a significant predictor of emergence (Fig. 3; Table 2). However, log seed mass did not predict emergence in soybean, common bean, or peanut (Fig. 3; Table 2). Domestication was a significant predictor of emergence in only two species (lentil and mung bean; Fig. 2; Table 2). However, with an additive model including seed mass and domestication, domestication did not significantly increase the likelihood of emergence in any species; in two species (cowpea and soybean), domestication significantly decreased emergence probability ($z=2.20$, 1.98 ; $P=0.028$, 0.048 respectively).

To estimate the effect of domestication on emergence depth via changes in seed size, all significant within-species relationships between seed mass and emergence depth (Fig. 3) were combined with the effects of domestication on seed mass

Table 2. Significance levels for factors predicting emergence in each species

The seed mass multiples compare landrace accessions with wild, based on data from germplasm databases as well as the authors' own measurements (see Supplementary Fig. S1 at JXB online). Changes in emergence depth were predicted from these using the fitted models of emergence depth on seed size.

Species	Significance of		Seed mass multiple	Predicted emergence depth change (cm)
	Seed mass	Domestication		
Lentil	$z=4.41$, $P=10^{-5***}$	$z=2.65$, $P=0.0080**$	4.1	10.1
Mung bean	$z=3.00$, $P=0.0027**$	$z=2.61$, $P=0.0088**$	2.2	2.2
Lima bean	$z=5.00$, $P=5.87 \times 10^{-7***}$	NS	3.2	3.6
Cowpea	$z=3.16$, $P=0.0016**$	NS	6.8	5.4
Pea	$z=2.14$, $P=0.032^*$	NS	1.5	5.4
Soybean	NS	NS	7.8	–
Common bean	NS	NS	3.6	–
Peanut	NS	NS	2.4	–

Asterisks indicated standard P -value thresholds.

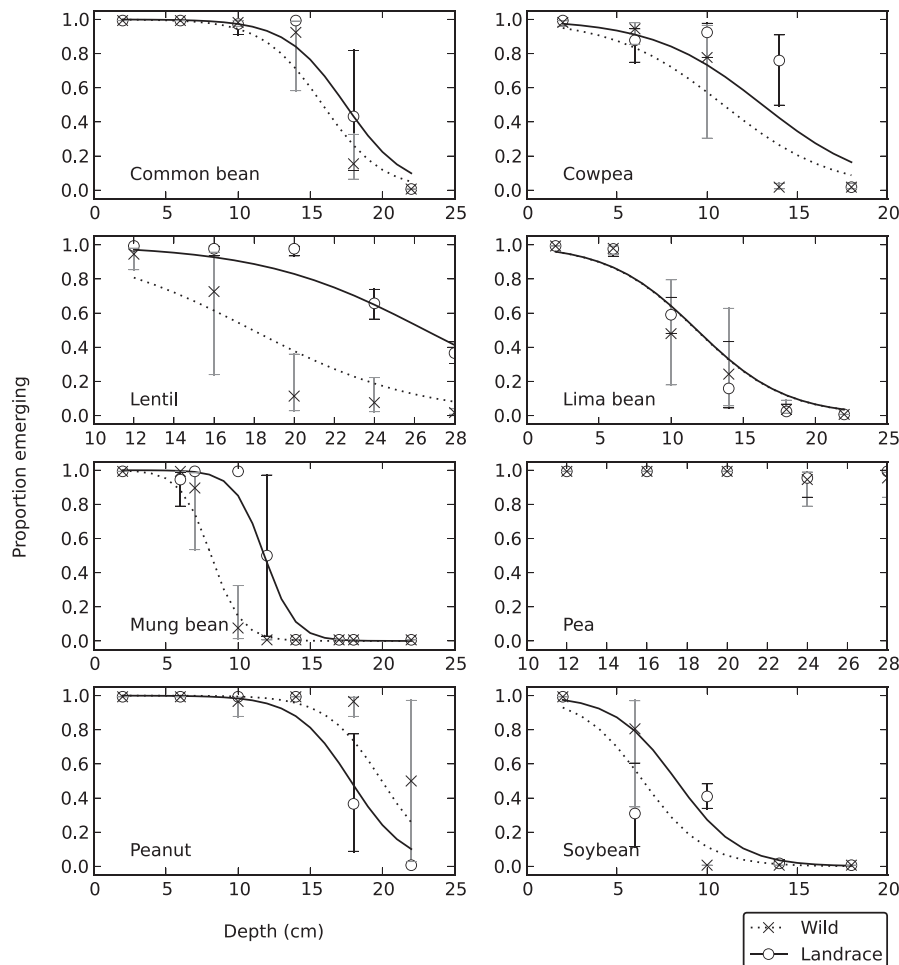


Fig. 2. Generalized linear model predictions of emergence probability against depth, according to domestication. Models fitted in R. Error bars represent the standard error of the mean as calculated on a logistic scale.

observed across a large number of accessions (Fig. 1). The increase in emergence depth predicted from increased seed size during domestication varied markedly across species, from 2.2 cm in mung bean to 10.1 cm in lentil (Table 2).

Survival

The survival analysis used time-to-emergence to investigate the effects of burial depth, seed mass, and domestication. It produced similar results to those of the simple binary (emerged/not emerged) analysis. Proportional hazard models assume a baseline ‘hazard function’—in this case, the probability of a seedling emerging on any given day—which is multiplicatively affected by ‘risk factors’, such as seed size. Larger seeds had a higher likelihood of emergence in three species (lentil, cowpea, and mung bean; $z=2.83\text{--}4.89$, $P=0.0046\text{--}1.1\times 10^{-5}$; lima bean was approaching significance). Domesticated seeds had a higher likelihood of emergence in just one species (lentil; $z=2.74$, $P=0.0062$).

Discussion

This work has provided the first general experimental test of the hypothesis that seed burial during early cultivation

exerted unconscious selection for larger seeds. Seed mass data for grain legumes spanning a global sample of independent centres of crop domestication conformed to the widely cited observation that larger seeds are one of the hallmarks of domestication (Harlan *et al.*, 1973; Smith, 2006; Purugganan and Fuller, 2009; Lee *et al.*, 2011) (Fig. 1). However, the experimental results only offer limited support for the burial depth hypothesis, finding a relationship between seed mass and emergence depth in some but not all of the species tested. The species in which neither seed size nor domestication affected emergence depth (common bean, peanut, and soybean) indicate that selection on emergence depth in cultivated grain legumes cannot have been a general phenomenon in cultivated grain legumes.

The archaeobotanical evidence for a number of species—including mung and urd beans, lentil, pea, soybean, and adzuki bean—suggests that a delay of some millennia between the earliest evidence of cultivation and an increase in seed size is a common pattern in legumes (Fuller, 2007). The present data suggest that this pattern cannot be explained by a common mechanism. Mung bean is one of two Indian *Vigna* species that have been studied to provide archaeobotanical

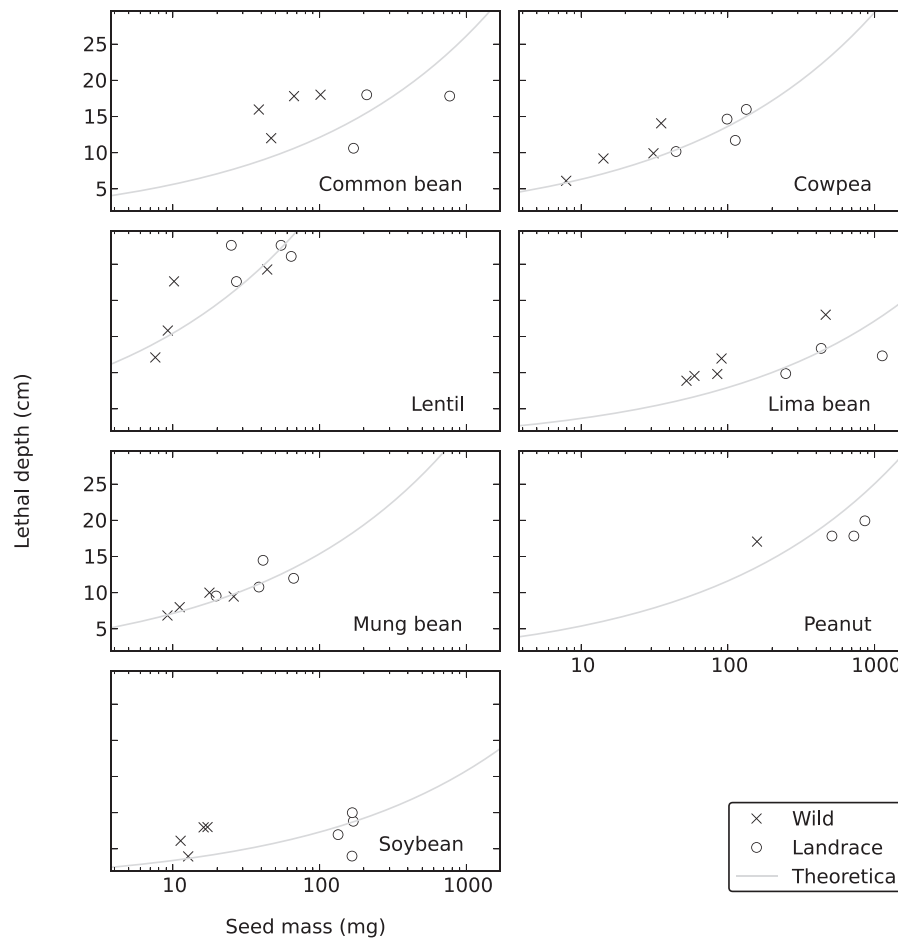


Fig. 3. The depth at which 50% of seeds for each accession are expected to emerge (from fitted generalized linear models), against the average mass of each accession. Data are excluded where it was not possible to fit a realistic lethal depth for an accession. The grey lines indicate the shape of a relationship of the form $\text{depth} \propto \sqrt[3]{\text{mass}}$ (predicted by theory), drawn through the centre of the points on each plot. In lentil, cowpea, and mung bean, the 95% confidence interval for the gradient on log–log axes includes 1/3 (corresponding to the cube-root relationship) and excludes 0. In common bean, peanut, and soybean, it includes 0 and excludes 1/3. In lima bean, the lower and upper bounds of the confidence interval are just below 0 and 1/3, respectively.

evidence for the hypothesis (Fuller and Harvey, 2006), and in this case it was found that both seed mass and domestication are predictors of emergence depth. The same is true of lentil, another species where archaeobotanical evidence has been interpreted in favour of the burial hypothesis (Fuller, 2007). The present data thus support the archaeobotanical evidence in these cases: any change in cultivation practices that led to the deeper burial of seeds, such as the introduction of animal-drawn ploughs, would have been able to drive some degree of selection on seed mass in mung bean and lentil, and perhaps also in lima bean, cowpea, and pea. However, soybean, common bean, and peanut showed no size-dependent response to depth, indicating that the increases in seed size associated with domestication in these species has another cause.

If selection had acted via burial depth, mechanisms other than seed size might have been expected also to respond, increasing emergence from depth beyond that expected from increased seed size alone. For example, increased allocation of resources to seedling shoot (versus root) growth can allow emergence from deeper burial (Seiwa *et al.*, 2002). There is

evidence from cassava (*Manihot esculenta* Crantz) that seeds can change between epigeal germination, where the cotyledons are lifted out of the soil, and hypogeal germination, where the cotyledons remain in the soil where the seed was planted, within the time scale of domestication (Pujol *et al.*, 2005); the significance of this for emergence depth is discussed below. However, this prediction was not borne out in any of the species tested: additive models including seed mass and domestication did not show an increase in emergence associated with domestication. In fact, domestication had the opposite effect for two species, with landrace seedlings less likely to emerge from a given depth than predicted on the basis of seed size.

Among the species tested, there was a marked difference between those with hypogeal germination, where the cotyledons remain in the soil as storage organs, and those germinating epigeally, raising the cotyledons to the soil surface where they have a photosynthetic role. Hypogeal species (lentils and peas) were best able to emerge from depth ($P=4 \times 10^{-3}$, adding a germination-type term to a mixed effects generalized linear

model), even though they were among the smaller seeds used. A likely explanation is that, not needing to pull their cotyledons through the soil, they could produce a thinner shoot, requiring a smaller investment of resources per unit depth.

Theoretically, maximum emergence depth is the length the shoot can grow from seed reserves, which is expected to be proportional to the cube-root of seed mass (Bond *et al.*, 1999). While some species, such as cowpea and lentil, appear to fit this pattern, others, such as common bean and soybean, show a smaller than expected change in emergence depth (Fig. 3). Most of the species tested are epigeal, and the cotyledons have a role in photosynthesis as well as storage. In those species with relatively modest increases in emergence depth, selection may be producing a greater allocation of resources to the photosynthetic role (i.e. cotyledon area), driving faster initial growth.

Seeds had a surprising ability to emerge from depth under the experimental conditions, with some hypogeal seedlings growing through 28 cm of soil (the greatest depth tested) to reach the surface. Human disturbance of the soil is unlikely to bury seeds to such depths. However, the conditions in this experiment (high moisture, homogeneous stone-free soil, small variance in temperature, and no competition) are expected to permit emergence from a greater depth than in the field. Few field experiments in the literature have tested such depths, although some tests on legume crops have shown no significant disadvantages to sowing depths down to 10 cm (Siddique *et al.*, 1997; Siddique and Loss, 1999). A study of weedy grasses found that the median lethal depth in the field was ~30% shallower than in the greenhouse (Dawson and Bruns, 1962). It is reasonable to assume that the differences in emergence depth which were the focus of this study would be similar, albeit of smaller magnitude, in the environment where selection could have acted on them.

Conclusion

Emergence depth increased with seed size in some crop species, but not others, indicating that selection did not act generally on emergence depth during the domestication of grain legumes. In lentil and mung bean especially, the results offer some support for the hypothesis arising from archaeobotanical data that deeper burial in cultivated fields was a selective pressure on seed size. In other species, particularly common bean, soybean, and peanut, the hypothesis is not supported. It is therefore concluded that other selection pressures were involved in the evolution of larger seeds during the domestication of grain legumes. Either another shared selection pressure drove the increase in seed size or, more plausibly, crops may have been subject to different selection pressures, and even multiple selection pressures acting in concert.

More generally, the present results are a reminder that different human and biological processes may well have acted in different places and on different crops (Harlan, 1992, p. 46; Marshall and Hildebrand, 2002; Meyer *et al.*, 2012), so that data on one species might not lead to a general theory that holds for all species. To distinguish general patterns in crop domestication from specific features of the history of particular plants, multiple species from independent centres of origin must be compared.

Supplementary data

Supplementary data are available at *JXB* online.

Figure S1. Emergence of planted seeds within a 5 week time span.

Supplementary file. Emergence data

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