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The Origins of Agriculture: Intentions and Consequences

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Abstract

We synthesise the results of a large programme of plant ecological research to investigate the selective pressures driving crop domestication and the origins of agriculture in western Asia. We explore this primarily through a series of experiments, comparing the ecological characteristics of: (1) domesticated cereal and pulse species with their wild progenitors and (2) the wild progenitor species with other west Asian grasses and legumes that did not become domesticated during the emergence of agriculture. In particular, we consider the balance between deliberate human selection and unintended consequences of human actions in driving the domestication process. Taken together, our results provide the first empirical evidence to suggest that ecological processes, and unintended selection due to competition between growing plants within anthropogenic environments, may have played a more significant part in the emergence of agriculture than previously supposed. Such human-plant co-evolutionary mechanisms would render unnecessary the search for ‘push’ or ‘pull’ factors, dependent on deliberate human invention to solve a problem or to satisfy a need, as prime movers to explain why hunter-gatherers switched to an agricultural way of life.

Keywords: plant domestication, unconscious selection, experiment, ecology, co-evolution

1. Introduction

The emergence of agriculture in southwest Asia marked a major change in human subsistence, whereby the hunting and gathering of wild food resources, which had persisted for millennia, was largely replaced by agricultural production. The reasons for this fundamental change have been the subject of a large body of research, much of which has been devoted to establishing why human populations chose to pursue an agricultural way of life. Suggested causes of the switch to agriculture have included ‘push’ factors such as deteriorating climate or demographic pressure (e.g. Bar-Yosef 2011; Cohen 2009) and ‘pull’ factors such as social pressure (e.g. Hayden 2009), but the extent to which this transition represents a deliberate invention to solve a particular problem or to satisfy a specific need is a subject of debate (see, for example, Rindos 1984; Abbo *et al.* 2011, 2012; Zeder 2015). Although the decision to cultivate (sow the seeds of) wild plants, or to exert some control over wild animals or their environment, are human choices, the intentions behind these decisions may be quite different to their ultimate consequences - domestication and dependence on agricultural production.

The idea that agriculture was an unintended consequence of human actions has a long history that can be traced back to Darwin, and this paper begins by reviewing previous ideas on the role of unconscious or unintended selection as a mechanism driving domestication and the emergence of agriculture. This is followed by an exploration of the selective pressures acting on plants in the lead up to crop domestication. To do this, we identified plant traits that distinguish domesticated crops from their modern wild counterparts and traits that distinguish between these ‘progenitor’ species and other west Asian species that were not domesticated during the emergence of agriculture. These traits represent the consequences of selection between wild species, and the subsequent evolutionary changes within species that gave rise to domesticated crops, and so may shed light on the nature of these selective pressures, whether intentional or unintentional.

2. Selective pressures and intentionality

Darwin (1859, 1868) distinguished between methodical selection of plant varieties and animal breeds, with the aim of modifying the species, and unconscious selection resulting from the preservation of valued individuals in the absence of any intention to achieve long-term change. The concept of unconscious (or automatic) selection has been taken further, however, by including in this category changes brought about by the transportation of plants (or their seeds) to new locations and anthropogenic environments, while treating any form of deliberate human selection of desirable traits or valued individuals as examples of conscious (or intentional) selection (Darlington 1963; Higgs and Jarman 1969; Harlan and de Wet 1973; Heiser 1988; Zohary 2004). Most of these authors accept that human selection pressures also contributed to the evolutionary process but, like Darwin, accord to unconscious/automatic selection a more central role in crop domestication, and suggest that such unintentional selection is likely to have been particularly important during the early stages in the emergence of agriculture. Higgs and Jarman (1969), however, argue that selection of domesticated traits may have occurred without the need for human intent, but rather through a symbiotic relationship between people and plants (or animals).

Rindos (1980, 1984) further developed the symbiotic approach in relation to plant domestication by proposing a co-evolutionary model to account for the emergence of agriculture that is not reliant on human foresight. This model places emphasis on positive feedback mechanisms, arguing that plants which responded positively to human exploitation or environmental manipulation, e.g. those that most benefitted from people as dispersal agents or from human-mediated growing conditions, increased in abundance, which in turn resulted in greater quantities of food being available to their human predators. Competition between plants would tend to favour those plants, and species, that are best suited to this developing mutualistic relationship, and those that are less well adapted would tend to be excluded, resulting in selection for particular phenotypic changes within species as well as increasing human dependence on fewer species. In this way, human activities, ranging from localised disturbance and nitrogen enrichment around human settlements to fire, tree felling and cultivation, provided the environment in which these selective pressures operated. As human attention became focussed on the plants that thrived in these anthropogenic environments, the time spent on other collecting activities would decline, so that cultivation gradually replaced collecting as the main subsistence activity (Rindos 1980, 1984).

More recently, the role that environmental manipulation plays in the process of domestication has been elaborated through niche construction theory. This emphasises the creation and development of the anthropogenic environment, initiated through human manipulations such as burning, woodland clearance, soil preparation and water management, while plants colonised these disturbed soils and took advantage of the newly created fertile habitats (Smith 2007, 2011, 2016; Zeder 2012, 2016). In this context, early attempts at cultivation can be seen as one type of human manipulation, within a broad range of strategies, where a wide range of species 'auditioned' as potential domesticates (Smith 2007). Zeder, although critical of Rindos' thesis, accepts the basic tenets of the co-evolutionary relationship between people and plants (as well as animals) but focuses on the creation and development of the anthropogenic environment, whereas Rindos emphasises the role of positive feedback processes. The major point of departure in their arguments lies in the way in which they treat intentionality. Neither Zeder nor Rindos suggest that people intended to domesticate plants or invent agriculture. However, for Zeder, the goal-oriented nature of human environmental manipulations is an essential element in the development of human-plant domestication relationships. Rindos, on the other hand, while not denying human intent and invention, argues that this is not a necessary component of the co-evolutionary process leading to domestication and agriculture. He contends that even if the intentions behind practices such as woodland clearance and cultivation were not directed at enhanced productivity or predictability – fires could be started to drive game, trees cut for building material, or seeds sown to relocate plants nearer to settlement – the effect of these actions on the environment would be the same, and the ultimate consequences well beyond the intended results of the actions.

Despite these differences, Zeder's and Rindos' ideas have much in common. Both see the domestication, and in Rindos' case the emergence of agriculture, as an outgrowth of co-evolutionary processes within the anthropogenic environment, and accord equal prominence to the role of people and plants in the development of this relationship. A similar approach is taken by Fuller *et al.* (2010) who consider some of the unintended entanglements between plants and people during domestication that might lead to labour ‘traps’ involving greater investment in crop processing and maintenance of soil fertility, balanced against the prize of higher yields. An arguably greater distinction is between these co-evolutionary models, on the one hand, and those assuming that the adoption of agriculture was a conscious decision and/or a response to environmental, demographic or social pressures, on the other (e.g. Moore and Hillman 1992; Bar-Yosef 2011; Cohen 1977, 2009; Bender 1978; Hayden 2009). These external ‘push’ and internal ‘pull’ models inevitably lead to a search for the reasons why people chose to domesticate plants or adopt agriculture, while the co-evolutionary frameworks are largely concerned with the interactions between people and plants *within* anthropogenic environments.

Intermediate positions between deliberate invention of agriculture and unconscious selection for certain plant characteristics have also been advocated. For example, optimal foraging theory (in particular the diet breadth model) has been proposed as an explanatory framework for the domestication of crops (Winterhalder and Kennett 2006; Gremillion and Piperno 2014). This model predicts that foragers will only utilise low ranked resources (such as wild grasses) – or invest in labour-intensive processing methods such as grinding, as evidenced by an increased use of grinding tools at this time (Wright 1994) – when faced with circumstances of resource depression (a lowered availability of more desirable, high ranking foods) due to environmental change or demographic pressure, which provides a possible explanation for the increased exploitation of wild grasses. More recently, Wood and Lenné (2018), have argued that the west Asian cereal progenitors would have been particularly attractive to seed gatherers as they had certain physical characteristics which enabled them to form pure dense stands. They then hypothesise that, as climate change reduced the area occupied by these wild stands, early plant gatherers chose to replicate the conditions favoured by these preferred species by sowing them in disturbed ground. Other models propose that low atmospheric carbon dioxide (CO_2) concentrations, and/or low temperatures and rainfall, during the last glacial period limited the productivity of plants, and so acted as a limiting factor on the emergence of agriculture (Sage 1995; Richerson et. al. 2001; Cunniff 2008, 2010, 2017; Kavanagh 2018; Piperno 2018). These models therefore see the subsequent amelioration of climatic conditions as facilitating a switch to agricultural production rather than agriculture being a response to deteriorating conditions.

While none of these models require foresight of the longer-term consequences of a greater focus on particular plant foods, they all rely on external factors to motivate a change in foraging patterns. Also, while they may provide a reasonable explanation for the introduction of crop progenitor species into the human diet (e.g. in the case of the diet breadth model), or an explanation of why agriculture did not happen earlier (e.g. in the case of the CO_2 limitation model), they do not explain how these changes led to the domestication of plant species, or the emergence of agriculture (Gremillion and Piperno 2009; Smith 2015; Zeder 2016). As such they address some of the pre-conditions for agriculture rather than its cause (Sage 1995; Cunniff 2010, Piperno 2018).

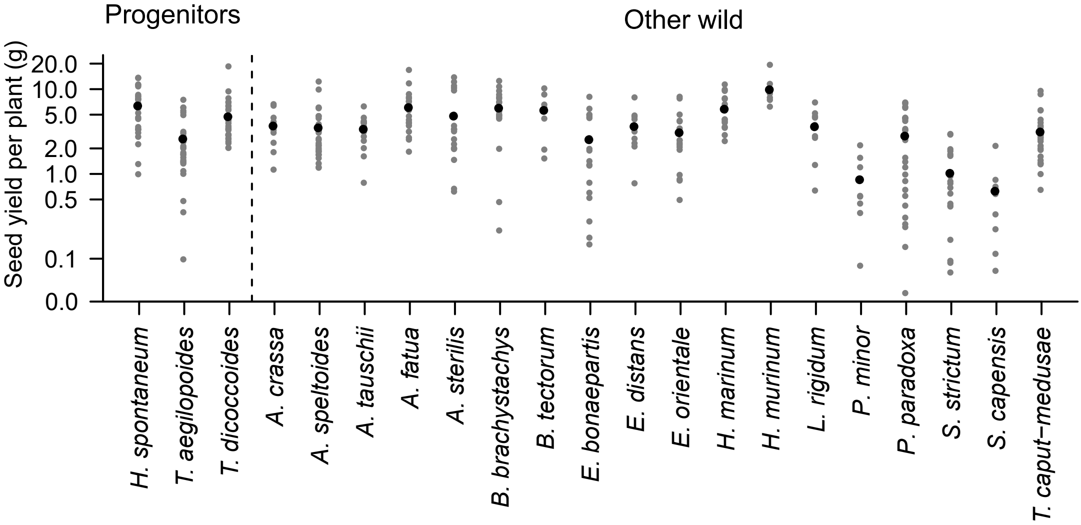
3. Selection of plant traits during domestication

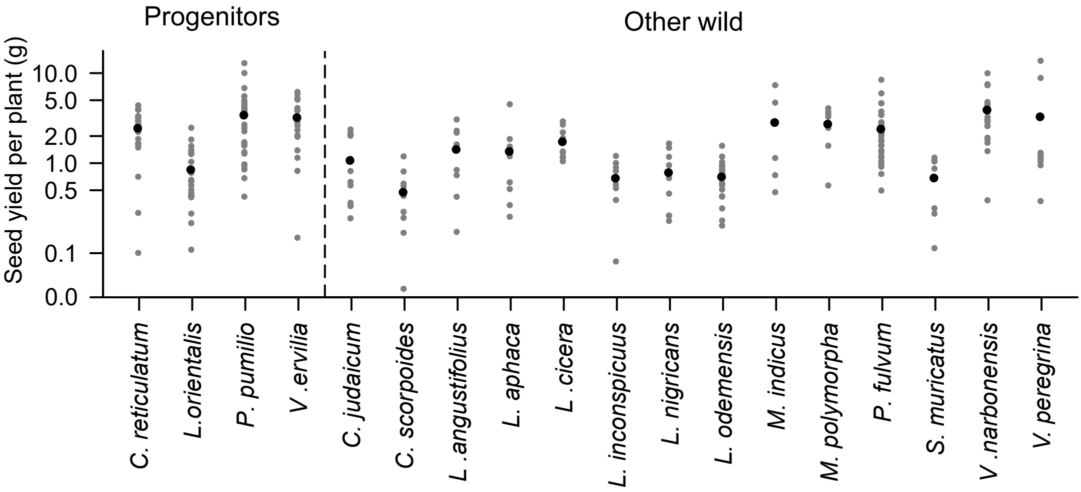
The research presented here synthesises the results of a series of ecological investigations designed to explore the selective pressures that operated on plant species during the process of domestication, with the aim of gaining a better understanding of the nature of selection and the likely causal mechanisms involved. In particular, we consider factors that may have influenced the selection and early evolution of plants in anthropogenic environments, prior to cultivation and in early cultivated plots. Selection during crop domestication (whether intentional or unintentional) operates at two levels: first, selection of the wild species that became domesticated and, secondly, selection resulting in the transformation from wild species to domesticated crop. We explore selection at both stages primarily through experimental ecology, comparing the ecological characteristics of: (1) domesticated cereal and pulse species with their wild 'progenitors' (i.e. those species most closely related to the domesticated species, and therefore the closest modern proxies for the original progenitors), and (2) the wild progenitor species with other west Asian grass and legume species that are thought to have been collected (Wallace *et al.* 2019) but did not become domesticated (see Supplementary Table 1 for a list of the species included in the experimental results presented here). A broad range of plant characteristics was considered, including vegetative characteristics as well as reproductive seed traits, in order to evaluate whether the characteristics selected during domestication best fit with intentional human selection for increased food yield or unintended selection relating to competition between plants within the anthropogenic environment.

A suite of plant characteristics that distinguish domesticated plants from their wild progenitors has been used to define a ‘domestication syndrome’ (Hammer 1984; Gepts 2004; Fuller 2007), one of which is larger seed size. It is commonly accepted that this increase in seed size was the result of intentional human selection, and also that wild species with large seeds would have been deliberately selected for cultivation over species with smaller seeds, as a means of maximising food yield (Ladizinsky 1975; Evans 1993), though Abbo *et al.* (2010) have argued that yield stability (which is not directly related to seed size) is likely to have been more important consideration for early cultivators than yield maximisation.

3.1 The relationship between seed size and total seed yield

To investigate the relationship of seed size to total seed yield in wild plant species, we conducted a series of experiments to compare the yield of the wild counterparts (likely progenitors) of cereal and pulse species domesticated in western Asia, with other wild grasses and legumes from the same region that were not domesticated (Cunniff *et al.* 2014; Preece *et al.* 2015). Initial experiments on nine species of wild grasses (three cereal crop progenitors and six grass species that were not domesticated) indicated that progenitor species were capable of producing a higher yield (based on the estimated number of seeds per plant and their average weight) than the wild species in the experiment (Cunniff *et al.* 2014). Later experiments (Preece *et al.* 2015) used a larger number of grass species (including the three progenitor species and 18 species that were not domesticated) as well as wild legume species (the progenitors of four pulse crops and 14 other legume species). Although the progenitor species had, on average, larger seeds, the wild crop progenitors of both cereal and pulse crops did not have greater total seed yield (based on the actual weight of harvested seeds) than the other wild species (Preece *et al.* 2015; Fig. 1). Indeed, some small-seeded grasses returned a higher yield relative to the mass of seed sown.


Progenitors
Other wild
Seed yield per plant (g)
20.0
10.0
5.0
2.0
1.0
0.5
0.1
0.0
H. spontaneum
T. aegilopoides
T. dicoccoides
A. crassa
A. speltoides
A. tauschii
A. fatua
A. sterilis
B. brachystachys
B. tectorum
E. bonaepartis
E. distans
E. orientale
H. marinum
H. murinum
L. rigidum
P. minor
P. paradoxa
S. strictum
S. capensis
T. caput−medusae


Progenitors
Other wild
Seed yield per plant (g)
10.0
5.0
2.0
1.0
0.5
0.1
0.0
C. reticulatum
L.orientalis
P. pumilio
V .ervilia
C. judaicum
C. scorpoides
L .angustifolius
L. aphaca
L .cicera
L. inconspicuus
L. nigricans
L. odemensis
M. indicus
M. polymorpha
P. fulvum
S. muricatus
V .narbonensis
V. peregrina

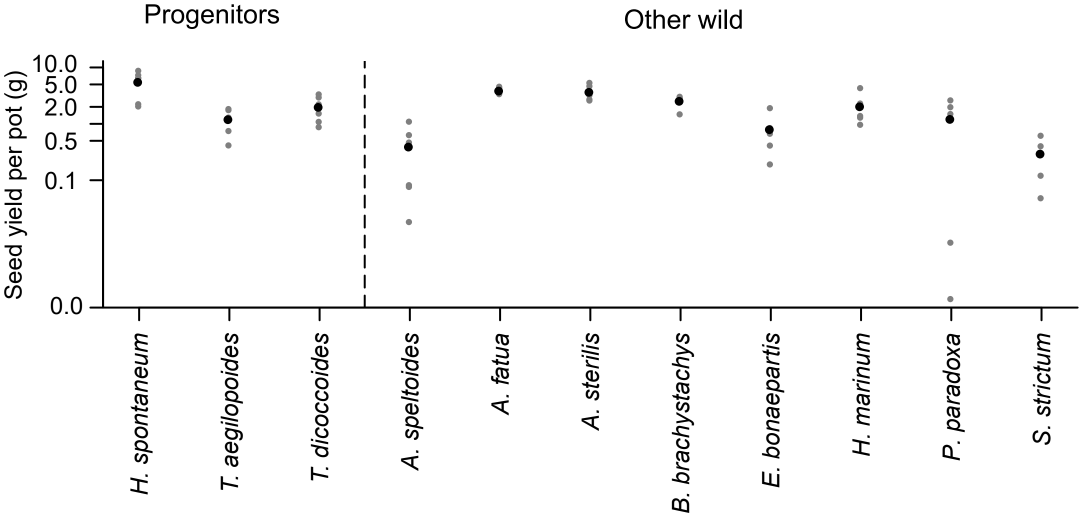

Progenitors
Other wild
Seed yield per pot (g)
10.0
5.0
2.0
0.5
0.1
0.0
H. spontaneum
T. aegilopoides
T. dicoccoides
A. speltoides
A. fatua
A. sterilis
B. brachystachys
E. bonaepartis
H. marinum
P. paradoxa
S. strictum

Figure 1. A comparison of seed yield for West Asian crop progenitors and other wild species of the region. Top: seed yield of individual grass plants; Middle: seed yield of individual legume plants; bottom: seed yield per unit area for grasses. Top and middle based on data from Preece *et al.* 2015; bottom based on data from Preece *et al.* 2018.

As seed yield per unit area may have been more important to early cultivators than yield per plant, we also investigated whether area yield is greater in cereal progenitors than other wild grass species when plants are grown in pure (single species) stands (Preece *et al.* 2018). Regardless of whether an equal mass of seeds or an equal number of seeds was sown for each species, the yield per unit area was not significantly greater in progenitors than in non-progenitor wild species, (Preece *et al.* 2018; Fig. 1). Our results do not therefore support the suggestion of a yield advantage for crop progenitors over other wild species. This suggests that factors other than intentional selection to improve seed yield were involved in the determination of which species were domesticated from amongst the wild species available to early cultivators, although many of these were in fact collected by pre-agricultural gatherers (Preece *et al.* 2015).

3.2 Seed size may have been influenced by factors other than yield maximisation

To explore the possibility that increased seed size may have been influenced by factors other than yield maximisation, we turned to vegetable crops that are harvested for their leaves, stems or roots, where seed size is not a component of overall food yield. We compared the seed mass of seven vegetable crops, which are thought to have been domesticated in antiquity, with that of their likely wild progenitors, and made the same comparisons for ten cereal and nine pulse crop progenitors and domesticates (Kluyver *et al.* 2017). We found that, for species from western Asia and Europe, the domesticated varieties are 20% to 1.7 times larger than their progenitors, which is comparable with the degree of seed enlargement for the west Asian cereal and pulse crops, which were 14 % to 4.1 times larger. Whatever the cause of the increased seed size in vegetable crops, it opens up the possibility that seed enlargement in grain crops was, at least partly, due to unintentional selection for larger seeds or larger plants in the cultivated plot (Kluyver *et al.* 2017). The same selection pressures that apply in the transition from progenitor to domesticate could also apply to selection between the gathered wild species that early cultivators attempted to grow.

3.3 Was larger seed size unconsciously selected by deeper burial under cultivation?

An early suggestion for how larger seed size may have been unconsciously selected in cultivated plots is that, because seeds are likely to be buried more deeply by human planting than they would be in the wild, there was selection for larger seed size due to the need for seedlings to emerge from a greater depth in the soil, which would require the larger food reserves provided by large seeds (Harlan and de Wet 1973; Zohary 2004; Fuller 2007; Purugganan and Fuller 2009). We tested this hypothesis through an experiment using eight pulse crop species, domesticated in six different regions, comparing seed size with ability to emerge from depth, both within each crop and between the domesticated forms and their wild progenitors (Kluyver *et al.* 2013). While seed mass was a significant predictor of emergence in five of these crops, domestication status (progenitor or domesticated) was a significant predictor in only two species (Kluyver *et al.* 2013). This indicates that although seed size is important for emergence from depth in some species, it is an unlikely general mechanism of selection for increasing seed size during the evolution from progenitor to domesticate, and it was concluded that other selective pressures were involved in seed enlargement during the domestication of pulse crops (Kluyver *et al.* 2013).

3.4 Functional traits of cereal crop progenitors compared with those of other wild grasses

In order to identify other selective pressures that may have been responsible for some species becoming domesticated and others not, our ecological experiments compared the functional traits of cereal crop progenitors with those of other west Asian wild grasses (Cunniff *et al.* 2014; Preece *et al.* 2015. The characteristics measured included seed mass, germination rate, seedling size, plant height and biomass, leaf area, relative growth rate, number of tillers, time to flowering, number of seeds, and resilience to defoliation. Our results demonstrated that, as well as larger seed mass, cereal crop progenitors germinate faster and have larger seedlings than the wild species in the experiments, as well as a greater resilience to defoliation. These characteristics could have conferred a selective advantage to crop progenitors in the fertile and disturbed anthropogenic environments surrounding early human settlements and in early cultivated plots. In some of these experiments, progenitors also tended to be taller (Cunniff *et al.* 2014), though in other experiments there were no significant differences in plant height or total above-ground biomass between progenitors and other wild grass species

(Preece *et al.* 2015, 2018). There were also no significant differences in plant height or biomass between progenitors and other wild legume species (Preece *et al.* 2015).

3.5 Functional traits of cereal and pulse crops compared with their wild progenitors

To investigate this further, we compared cereal and pulse crops domesticated in western Asia with their wild progenitors, considering whole-plant characteristics as well as reproductive seed traits, and found a strong positive correlation between seed size, final plant size and seed yield, with all three characteristics being greater in crops than progenitors (Preece *et al.* 2017; Fig. 2). This confirms previous observations (Schwanitz 1966), and suggests selection for large size acting on the growth of the whole plant during domestication. These results are consistent with other research, comparing a diverse selection of crop species with their wild progenitors, which also indicated that, as well as larger seeds, domesticates have greater above-ground biomass with larger leaves, and so greater light-capturing capability (Milla and Matesanz 2017), as well as greater total dry plant mass (Martín-Robles *et al.* 2018).

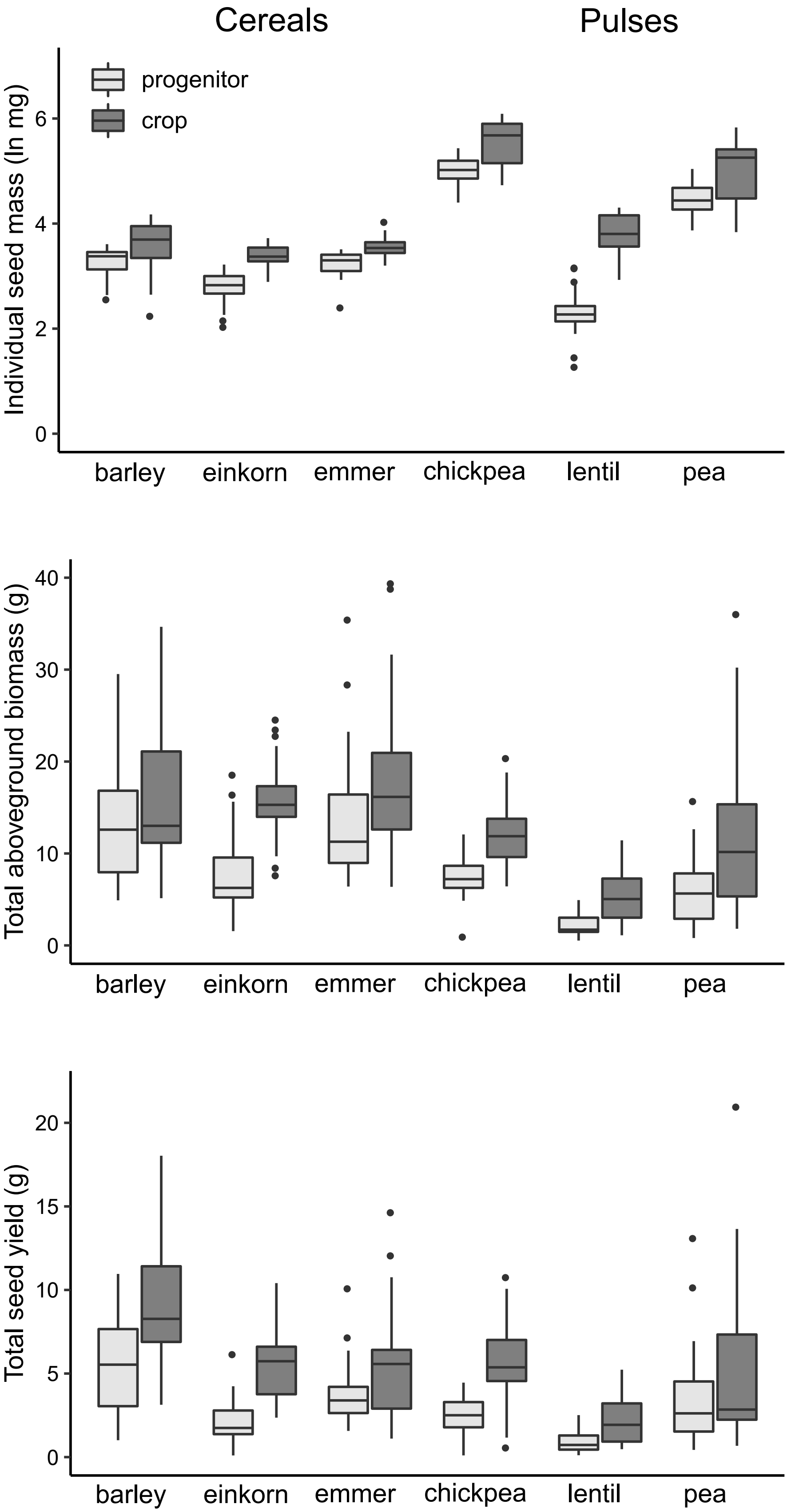

Cereals
Pulses
progenitor
crop
Individual seed mass (ln mg)
0
2
4
6
barley
einkorn
emmer
chickpea
lentil
pea
Total aboveground biomass (g)
0
10
20
30
40
barley
einkorn
emmer
chickpea
lentil
pea
Total seed yield (g)
0
5
10
15
20
barley
einkorn
emmer
chickpea
lentil
pea

Figure 2. A comparison of individual seed mass, total seed yield and above ground biomass for west Asian progenitor and domesticated species, showing the median, interquartile range, maximum and minimum values (excluding outliers), plus individual outliers. Based on data from Preece *et al.* 2017.

In a global comparison of herbaceous crops with wild herbaceous species, the domesticated crops were again observed to have tall canopies and a high leaf nitrogen concentration, indicating that they are fast-growing species and proficient competitors in resource abundant environments, such as would be found in intensively managed cultivation plots (Milla *et al.* 2018). Moreover, the crops occupied only a portion of the phenotypic space of the wild herbaceous plants with regard to these characteristics, suggesting habitat filtering whereby certain plant characteristics are selected in response to the conditions in a particular habitat niche (Milla *et al.* 2018). In addition, a comparison of 30 crop species, their wild progenitors and other wild herbaceous plants, found that progenitor species had root traits (thicker and less dense than those of other wild species) typical of fast-growing species with resource acquisitive strategies, that are adapted to fertile conditions (Martín-Robles *et al.* 2018). Crops displayed no consistent difference in root traits compared with their wild progenitors suggesting the early selection of wild progenitors that were already pre-adapted to fertile agricultural conditions, rather than further evolution of root traits under domestication (Martín-Robles *et al.* 2018).

Comparisons			Plants used	Result	References
	Crop progenitors	Other wild plants	Grasses	Estimated seed yield potentially greater in progenitors	Cunniff *et al.* 2014
	Crop progenitors	Other wild plants	Grasses and legumes	With a larger sample, measured seed yield not greater in progenitors	Preece *et al.* 2015
	Crop progenitors	Other wild plants	Grasses	Area seed yield not greater in progenitors	Preece *et al.* 2018
Domesticated crops	Crop progenitors		Seed crops and vegetables	Seeds of both vegetable and seed crops larger than those of progenitors	Kluyver *et al.* 2017
Domesticated crops	Crop progenitors		Legumes	Domesticates not consistently capable of emergence from greater depth of soil	Kluyver *et al.* 2013
	Crop progenitors	Other wild plants	Grasses	Progenitors germinate faster and have larger seedlings	Cunniff *et al.* 2014
	Crop progenitors	Other wild plants	Grasses and legumes	Mature plant size not consistently larger in progenitors	Cunniff *et al.* 2014 Preece *et al.* 2015
Domesticated crops	Crop progenitors		Grasses and legumes	Seed size, plant size and seed yield all greater in domesticated crops	Preece *et al.* 2017
Domesticated crops	Crop progenitors		Herbaceous plants	Plant size and leaf nitrogen content greater in domesticated crops	Milla *et al.* 2018
Domesticated crops	Crop progenitors	Other wild plants	Herbaceous plants	Root traits of progenitors and domesticates more resource acquisitive	Martín-Robles *et al.* 2018

Table 1 Summary of results

4. Discussion and conclusions

4.1 The plant ecological evidence

This study brings together a large body of experimental results (summarised in Table 1) which together provide the first empirical evidence to suggest that ecological processes played a significant part in plant domestication and the origins of agriculture. A clear trend to emerge from these ecological experiments is that size is an important factor both in the selection of crop progenitors over other wild species and in the changes associated with the process of domestication within species (Cunniff *et al.* 2014; Preece *et al.* 2015, 2017; Milla and Mantesanz 2017; Milla *et al.* 2018; Martín-Robles *et al.* 2018). These size differences are manifested in multiple plant organs (leaves, roots, seeds, as well as whole plants) and are closely interrelated, making it difficult to determine whether this selection acted primarily on the seed leading to larger plants, or on the growing plant leading to the production of larger seeds, or both. Yet this is an important distinction for archaeologists attempting to understand the relative roles of deliberate human selection for increased food yield and unintended selection relating to competition between plants within the anthropogenic environment.

Our experimental evidence suggests, however, that the larger seed size of progenitor species does not translate into greater yield either per plant or per unit area (Preece *et al.* 2015, 2017) and that increased seed size during domestication also occurs in species where the seed is not the part of the plant used for food (Kluyver *et al.* 2017), both of which suggest that the seed may not be the primary object of deliberate human selection. We have also found limited evidence for selection (intended or unintended) of progenitor species because their large seeds conferred a greater ability to produce seedlings that emerge from greater depth of burial. Nevertheless, crop progenitors germinate faster and have larger seedlings than wild species that were not domesticated, as well as root systems that would be expected to confer a competitive advantage in fertile, disturbed habitats (Martín-Robles *et al.* 2018). These attributes would give them a head start in the competitive arena of the cultivated plot (aptly described as a botanical battleground by M. Jones (1988)) and in other anthropogenically disturbed environments (Harlan 1973; Cunniff et al. 2014). There is also increasing evidence for selection during domestication for a suite of traits (such as larger leaves, final plant size and above-ground biomass) that would place plants at a continuing competitive advantage in resource abundant environments (Preece *et al.* 2017; Milla and Matesanz 2017). Finally, seed crop species exhibit a subsample of the phenotypic variation within wild herbaceous species (Milla *et al.* 2018) suggesting habitat filtering, which is consistent with competition between species.

The experimental evidence also indicates that different plant traits may have been selected for at different stages of the domestication process. Differences between crop progenitors and other wild species suggest that rapid germination and early growth rate may have been particularly advantageous attributes during the early competitive selection of wild species as successful crops, while increases in whole plant size and photosynthetic capacity may have been more instrumental in the transformation from wild progenitor to domesticated crop.

4.2 Implications for understanding the origins of agriculture

These results have implications for our understanding of how and why agriculture emerged in Western Asia, a debate that has become somewhat polarised in recent years. This is partly because different researchers have tended to focus on different aspects of the domestication process: deliberate human actions or other selective pressures acting on the results of these actions. Both are essential components of the process – without human agency, for example, there would be no anthropogenic environment. In this paper, we have been primarily concerned with exploring the potential role of unintended selective pressures in the evolutionary processes leading to domestication, as these have been relatively little studied compared to the search for possible reasons to explain why people would chose agriculture (Abbo and Gopher 2017). This is not to say that hunter-gatherer populations had no knowledge of plant reproductive cycles, or were incapable of recognising potentially useful plant characteristics (compare, for example, Abbo and Gopher 2017; Brown 2018). What is more debatable, however, is whether human populations engaged primarily in hunting and gathering had the foresight to appreciate the more far-reaching consequences of their interventions, and so whether these ultimate consequences were what they intended to achieve through their proximate actions. In this context it is also important to consider that plants, while not conscious actors, also have agency in the sense that, in a co-evolutionary relationship, their response to human manipulations may affect the subsequent actions and decisions of people (van der Veen 2018).

By demonstrating that domestication was potentially driven by co-evolutionary forces operating on growing plants in anthropogenic environments, rather than by selective pressures that are dependent on deliberate human intentions, the need to identify push or pull factors as prime movers to explain why people turned to agriculture may be rendered unnecessary. Rather than seeing intentional and unintentional selection in opposition to one another, however, a more fruitful line of enquiry is to consider their relative contributions to agricultural origins. One implication of our findings is that the pace of the domestication process may have been dependent on the relative roles of human intent (to improve yield etc.), which might be expected to result in rapid change, and the selective pressures acting on growing plants in the anthropogenic environment, which are likely to proceed more slowly. In this context, a significant role for unintended selection as a driving force in the origins of agriculture may be indicated by the mounting evidence that domestication was a protracted process (Tanno and Willcox 2006; Purugganan and Fuller 2011; Fuller *et al.* 2012, 2014; Allaby *et al.* 2017; Purugganan 2019) though this itself is a contested issue (Abbo *et al.* 2012; Abbo and Gopher 2017). It has also been suggested (Fuller *et al.* 2010) that the first steps to agriculture may have been taken with a view to gains in terms of increased yield, and that it was only later that farmers fell into the trap of greater labour costs. The experimental evidence presented here, however, indicates that increased yield is not an automatic result of selection for greater seed size. This, and the potential of other ecological processes to effect change, supports an alternative suggestion that unintentional selection played a greater part in the early stages of domestication and that intentional human choices were of greater significance in the later stages of agricultural development, when some of the benefits of agriculture (such as the greater productivity of domesticated plants) became more apparent.

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Author contributions

GJ, CPO, MC and MR conceived the project. CP, JS and TK performed the experiments and, with CPO and MR, conducted the statistical analyses. GJ wrote a first draft of the paper. All authors contributed to the writing of, and approved, the final version.

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Supplementary information

SPECIES	REFERENCES
Domesticated species	
Cereals	
Hordeum vulgare subsp. *vulgare*	Kluyver et al. 2017; Preece et al. 2017
Triticum monococcum subsp. *monococcum*	Kluyver et al. 2017; Preece et al. 2017
Triticum turgidum subsp. *dicoccum*	Kluyver et al. 2017; Preece et al. 2017
Pulses	
*Arachis hypogaea**	Kluyver et al. 2013
Cicer reticulatum	Kluyver et al. 2017; Preece et al. 2017
*Glycine max**	Kluyver et al. 2013
Lens culinaris subsp. *culinaris*	Kluyver et al. 2013, 2017; Preece et al. 2017
*Phaseolus lunatus**	Kluyver et al. 2013
*Phaseolus vulgaris**	Kluyver et al. 2013
Pisum sativum subsp. *sativum*	Kluyver et al. 2013, 2017; Preece et al. 2017
*Vigna radiata**	Kluyver et al. 2013
*Vigna unguiculata**	Kluyver et al. 2013
Progenitor species	
Grasses	
Hordeum vulgare subsp. *spontaneum*	Cunniff et al. 2014; Kluyver et al. 2017; Preece et al. 2015, 2017, 2018
Triticum monococcum subsp. *aegilopoides*	Cunniff et al. 2014; Kluyver et al. 2017; Preece et al. 2015, 2017, 2018
Triticum turgidum subsp. *dicoccoides*	Cunniff et al. 2014; Kluyver et al. 2017; Preece et al. 2015, 2017, 2018
Legumes	
*Arachis monticola**	Kluyver et al. 2013
Cicer reticulatum	Kluyver et al. 2017; Preece et al. 2015, 2017
*Glycine soja**	Kluyver et al. 2013
Lens culinaris subsp. *orientalis*	Kluyver et al. 2013, 2017; Preece et al. 2015, 2017
*Phaseolus lunatus**	Kluyver et al. 2013
Phaseolus vulgaris var. *aborigineus**	Kluyver et al. 2013
Pisum sativum subsp. *elatius* var. *pumilio*	Kluyver et al. 2013, 2017; Preece et al. 2015, 2017

Vicia ervilia	Preece et al. 2015, 2017
*Vigna radiata**	Kluyver et al. 2013
*Vigna unguiculata**	Kluyver et al. 2013
Other wild species	
Grasses	
Aegilops crassa	Cunniff et al. 2014; Preece et al. 2015
Aegilops speltoides	Cunniff et al. 2014; Preece et al. 2015, 2018
Aegilops tauschii	Cunniff et al. 2014; Preece et al. 2015
Avena fatua	Preece et al. 2015, 2018
Avena sterilis	Preece et al. 2015, 2018
Bromus brachystachys	Preece et al. 2015, 2018
Bromus tectorum	Preece et al. 2015
Eremopyrum bonaepartis	Cunniff et al. 2014; Preece et al. 2015, 2018
Eremopyrum distans	Cunniff et al. 2014; Preece et al. 2015
Eremopyrum orientale	Preece et al. 2015
Hordeum marinum	Preece et al. 2015, 2018
Hordeum murinum	Preece et al. 2015
Lolium rigidum	Preece et al. 2015
Phalaris minor	Preece et al. 2015
Phalaris paradoxa	Preece et al. 2015, 2018
Secale strictum	Preece et al. 2015, 2018
Stipa capensis	Preece et al. 2015
Taeniatherum caput-medusae	Cunniff et al. 2014; Preece et al. 2015
Legumes	
Cicer judaicum	Preece et al. 2015
Coronilla scorpioides	Preece et al. 2015
Lathyrus aphaca	Preece et al. 2015
Lathryus cicera	Preece et al. 2015
Lathyrus inconspicuus	Preece et al. 2015
Lens nigricans	Preece et al. 2015
Lens odemensis	Preece et al. 2015
Lupinus angustifolius	Preece et al. 2015
Medicago polymorpha	Preece et al. 2015
Melilotus indicus	Preece et al. 2015

Pisum fulvum	Preece et al. 2015
Scorpiurus muricatus	Preece et al. 2015
Vicia narbonensis	Preece et al. 2015
Vicia peregrina	Preece et al. 2015

Supplementary Table 1. List of species included in the experimental results presented here.

*Species domesticated outside western Asia.