

Functional attributes as a tool for understanding the process of cereal and pulse domestication

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Abstract

This thesis has sought to identify the selective pressures, both natural and anthropogenic, that led to cereal and pulse domestication in the Early Neolithic using a functional ecological approach. This was achieved through the identification of functional traits, which enabled certain species to thrive in response to the ecological selection pressures attendant on the climatic constraints the Late Pleistocene/early Holocene transition and on those of the anthropogenic environment in which domestication arose. Those traits that would best capture plant responses to these selection pressures were chosen, and relate to resource acquisition (responses to fertility and disturbance) and water-use efficiency (drought tolerance). The traits used comprise leaf dry matter content, specific leaf area, leaf area:thickness, stomatal density and length, canopy height and diameter, and genome size. The analyses of plants grown in natural habitats and those grown under experimental conditions show that these traits are robust across varying environmental conditions.

The research presented here demonstrates that there are traits that consistently differentiate domesticated cereal and pea crops and their wild progenitors from other wild grasses and legumes that were not domesticated. This thesis also demonstrates that not all Neolithic crops have the same responses to fertile conditions and drought tolerance. Examination of the functional traits indicates that domesticated barley, einkorn, emmer and pea and their progenitors, were physiologically predisposed to have a competitive advantage over other wild grass and legume species under fertile and moist conditions. The climatic amelioration associated with the early Holocene, and the engineered habitats associated with early Neolithic settlements and cultivation, favoured the competitive wild progenitors of the Neolithic cereal and pea crops. This competitive advantage for resource acquisition under productive conditions may have continued to be a significant selection pressure in early crop evolution. Lentil and chickpea are less competitive, however, and chickpea is less sensitive to droughted conditions compared to the other Neolithic crops. Lentil and chickpea may have enabled less fertile areas to be productive under cultivation, and chickpea potentially provided a buffer against crop failure during episodes of drought, to which cereal and pea crops are more susceptible.

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Appendix A

Appendix B

Chapter 1: Introduction

1.1 Introduction

Agriculture underpins complex societies and is the basis for the development of urban civilisations (Miller and Wetterstrom, 2000, Marston, 2017). It is through the capacity to generate food surpluses, sufficient to divert labour to non-food producing occupations, that agricultural economies enable specialisation and diversification of crafts and trades (Maisels, 1993). Agriculture developed independently in multiple locations worldwide (Cohen, 1977, Byrne, 1987, Blumler, 1996, Gepts, 2004, Purugganan and Fuller, 2009) with relative synchronicity between 13-4 kyr BP (Blumler et al., 1991, Blumler, 1996, Harris, 2004, Purugganan and Fuller, 2009). Confirmed primary centres of agriculture have been identified in at least seven different regions in the New and Old World, notably northeast North America, Mesoamerica, the Andes of South America, southwest Asia, Africa, southern China and southeast Asia (Gepts, 2004, p. 7, Purugganan and Fuller, 2009: Figure 1). The term agriculture is used here to describe an economic system that is based on the cultivation of crops and raising of livestock (following Harris, 2007, p. 29). This thesis will focus on the origins of plant agriculture in southwest Asia, a centre of origin that has provided some of the earliest evidence for agriculture (Harris, 2004, p. 13). Cultivation is defined here as is the deliberate planting and growing of crops, while domestication is a term applied to the process of genetic selection whereby the phenotypic characteristics of wild plants were transformed into those of crop plants.

Archaeobotanical remains recovered from early farming sites in southwest Asia provide the primary evidence for the domestication of crop species, in particular cereals and pulses, principally in the form of diagnostic rough-type abscission scars on cereal rachis remains (indicating a non-shattering ear, and so loss of natural dispersal mechanism) or changes in seed size. Loss of wild-type seed dispersal (non-shattering cereal rachis, or in the case of pulses, pods) and increases in seed size are amongst a suite of plant traits associated with domestication that are commonly referred to as the 'domestication syndrome', a term first coined by Hammer (1984). The loss of wild-type seed dispersal is often seen as a key trait indicative of domestication, due to the fact that plants are then rendered dependent on humans for their propagation (Hillman and Davies, 1992). Other characteristics typically included in the domestication syndrome are reduction of wild-type dispersal or burial aids (such as awns and spines), reduction of germination inhibition, synchronous tillering and ripening, and increased apical dominance with reduced lateral branching or tillering (Hillman

and Davies, 1992, Fuller, 2007, Fuller et al., 2012). These other traits, however, are not identifiable archaeologically, and legume pods rarely survive in the archaeobotanical record (Tanno and Willcox, 2006b). Causes for changes in seed size can also be ambiguous, due to the effects of environmental conditions such as precipitation, temperature, soil fertility and disturbance (Willcox, 2004, Ferrio et al., 2006, pp. 323-324, Cunniff et al., 2010, 2017), or vegetation dynamics such as stand density, inter-specific competition (Wilcox, 2004), or global climate, in particular increases in atmospheric carbon dioxide.

Archaeobotanical assemblages recovered from early farming sites not only provide visible evidence for domestication (i.e. traits associated with the 'domestication syndrome'), but are important for understanding the processes and selective pressures acting on plants during their domestication as crops, which resulted in the establishment of a new ecological niche, the crop field. The research in this thesis takes a 'plant-centred' approach (Cunniff, 2009), using principles of ecology as a means for understanding the selective pressures that were acting on wild crop progenitors and other wild species that were potentially exploited during the transition from foraging to farming. More specifically, the research presented here uses a functional ecological approach to identify which plant traits (measureable morphological, physiological or phenological features that relate to a plant's fitness (Violle et al., 2007)) distinguish wild species that were domesticated (progenitors) from those that were not, and to identify changes in the former during domestication. This will enable greater insight into the responses of plants to biotic and abiotic selection pressures associated with their exploitation and early cultivation. An advantage of functional ecology is that this approach is not reliant on whether or not visible plant traits are preserved in the archaeobotanical material, but rather it is based on characteristics of the species that can be measured on modern specimens, and extrapolated to the same species in the archaeobotanical record.

The rest of this chapter outlines proposed explanations for the emergence of agriculture within southwest Asia and discusses the concept of functional ecology, with reference to its applicability for understanding the process of plant domestication. The chapter concludes by presenting the research aims and objectives and a summary of the thesis structure.

1.2 Temporal and spatial context of plant domestication

Agriculture in southwest Asia originated in the region known as the Fertile Crescent, which refers to an arc that stretches across parts of present-day Israel, Palestine, Jordan, Lebanon, Syria, Turkey, Iraq and Iran (Figure 1.1). The process of plant domestication in this region encompasses the transition from complex, semi-sedentary hunter-gatherer groups during the Late Epipalaeolithic, with possible pre-domestication cultivation, through to the domestication of cereals and pulses and the appearance of sedentary farming communities in the Early Neolithic (Pre-Pottery Neolithic). During the Late Epipalaeolithic hunter-gatherers collected a range of wild plant species, including cereals and pulses (Savard et al., 2006, Weiss et al., 2006, Willcox et al., 2008, Colledge and Conolly, 2010, Asouti and Fuller, 2011, Weide et al., 2018). By the mid-11th millennium BP, the first unequivocal evidence for domesticated plants in southwest Asia appears at a number of sites, and soon after this (10.4-10.1 kyr cal. BP) the 'Neolithic package' of 'founder' crops was established (Zohary et al., 2012).

The identification of where, within the extensive and geographically diverse region encompassed by the Fertile Crescent, cereals and pulses were first domesticated has been a major focus of archaeological research (Vavilov, 1951, Helback, 1959, Harlan, 1971, 1992, Willcox, 2005, Brown et al., 2009, Abbo et al., 2010a, Fuller et al., 2011, 2012, Zohary et al., 2012). Consensus about the geographic origins of plant domestication in southwest Asia is currently somewhat elusive, as the probable locations(s), number of domestication episodes and rates of domestication for cereals and pulses are still under active debate (see Abbo and Gopher, 2017). It is beyond the scope of this thesis to contribute to the debate regarding the geographic origins of plant domestication within the Fertile Crescent, but current models are outlined here in order to place this research in context. Various models have been proposed and opinions tend to be polarised between hypotheses supporting a 'core' area within southeastern Turkey for all of the southwest Asian Neolithic grain crops (e.g. Lev-Yadun et al., 2000, Abbo et al., 2001, Gopher et al., 2001, Abbo et al., 2010a), followed by the dispersal of cultivars in all directions across the Fertile Crescent (Gopher et al., 2001), and those advocating multiple locations across the Fertile Crescent (i.e. diffused domestication e.g. Willcox, 2005, Morrell and Clegg, 2007, Brown et al., 2009, Fuller et al., 2011, 2012).

The 'core area' model for plant domestication is a concept first proposed by Braidwood (1960, 1975) that has since been developed based on surveys of present-day distributions of wild crop progenitors (e.g. Harlan and Zohary, 1966, Zohary and Hopf, 2000) and genetic studies of modern landraces (e.g. Heun et al., 1997, Badr et al., 2000, Özkan et al., 2002, Salamini et al., 2002). Proponents of the 'core area' hypothesis propose that each Neolithic grain crop arose from single, or a very limited number of, domestication events (i.e. monophyletic domestication) (Zohary, 1996, 1999, Abbo et al., 2010a, 2011a, 2013a). Proponents of the 'core area' model also tend to support the hypothesis of a rapid process of domestication (Abbo et al., 2011b, Peleg et al., 2011). It has been argued that a rapid process of domestication was necessary for the fixation of crucial domestication traits, such as nonshattering rachis types in cereals (e.g. Abbo et al., 2012) or loss of seed dormancy in pulses

(e.g. Ladizinsky, 1987, Abbo et al., 2009, 2011b). These rapid/core models also tend to favour the theory that conscious selection pressures played an important role in the process of domestication, in order to achieve fixation of certain domestication traits (Abbo et al., 2009, 2011b, 2012, 2014).

Counter to the 'core area' model, there is the school of thought that favours the model for diffused domestication (Higgs and Jarman, 1969, Willcox, 2005, Weiss et al., 2006, Fuller et al., 2012, Brown et al., 2009, Allaby et al., 2010, Zeder, 2011). Support for this model is based on archaeobotanical evidence for domestication from sites outside of the 'core' area in southeastern Turkey (e.g. Willcox, 2005, Weiss et al., 2006, Riehl et al., 2013, Weide et al., 2017, Colledge et al., 2018) and further genetic studies (see Allaby et al., 1999, 2008, Molina-Cano et al., 2005, Morrell and Clegg, 2007). Proponents of the diffuse model also tend to support the hypothesis that domestication was a protracted process that took place over several millennia (e.g. Tanno and Willcox, 2006a, Weiss et al., 2006, Fuller, 2007, Fuller et al., 2012, Allaby et al., 2008). This model is sometimes associated with natural (as opposed to artificial/deliberate) selection pressures (Tanno and Willcox, 2006a, Allaby et al., 2008), and therefore can accommodate the fact that domestication traits were not necessarily visible in the early stages of plant domestication (Tanno and Willcox, 2006a, Fuller, 2007). Another consideration is that activities relating to early plant management strategies and cultivation, such as the mode of harvesting or replenishment of seed stocks from wild stands, potentially increases genetic diversity and slows the process of trait fixation (Willcox, 2005, Fuller et al., 2012, p. 625).

1.3 Explanations for the emergence of plant domestication and the origins of agriculture

1.3.1 Proposed explanations for the origins of agriculture

Identifying the driving forces behind the transition from food gathering to food production during the Late Epipalaeolithic and Early Neolithic periods has generated a large body of (sometimes conflicting) research (e.g. Darwin, 1868, de Candolle, 2011, Vavilov, 1951, Engelbrecht, 1916, Harlan and de Wet, 1965, Zohary and Hopf, 2000). These studies have variously expanded and challenged theories for how and why plants became domesticated. At the broadest level, some argue for a deliberate (i.e. conscious) decision to domesticate plants and others for unintended (or unconscious) selection processes that led to plants becoming domesticated. In this section, these views for how and why cereals and pulses were domesticated in southwest Asia are discussed.

Within the debating arena for conscious selection, support is further divided between 'push' models (external pressures) and 'pull' models (internal pressures) as the drivers for this process. The push models hinge on external pressures, such as climate (e.g. Childe, 1928, Hillman et al., 2001, Gupta, 2004, Willcox et al., 2009, Bar-Yosef, 2011, 2017) or an imbalance of resources and demand caused by population pressure (e.g. Binford, 1968, Cohen, 1977, 2009). Push models have also been used to account for the relative synchronicity for the emergence of independent centres of agriculture worldwide. Climatic push models for plant domestication have long been advocated, such as Childe's (1928) 'oasis theory' that sees domestication in southwest Asia as arising due to droughted conditions associated with the Late Pleistocene, which forced humans, plants and animals together, resulting in familiarity between species that evolved into domestication.

Latterly, some scholars have suggested that the cold, arid conditions of the Younger Dryas associated with the glacial terminal triggered resource intensification, notably predomestication cultivation, in order to compensate for the reduction in wild resources (e.g. Moore and Hillman, 1992, Wright, 1994, Hillman et al., 2001). Moore and Hillman (1992) draw on changing ratios of arboreal to non-arboreal pollen from palynological records from Lake Huleh, Israel (analysed by Baruch and Bottema, 1991), in the context of archaeobotanical evidence for changes in subsistence strategies from Abu Hureyra, Syria. A marked decline in arboreal pollen from Lake Huleh, and a dramatic drop in the occurrence of plant remains potentially exploited from forest and forest fringe habitats from Abu Hureyra Phase 1 (including tree fruits such as pistachio and acorns, wild cereals and other wild grasses), coincides with the Younger Dryas (Moore and Hillman, 1992). They propose that the arid conditions of the Younger Dryas led to a retraction of the resource-rich forest and forest-fringe habitats and expansion of steppic grasslands, leading to an imbalance in resource and population demands (Moore and Hillman, 1992, Hillman et al., 2001). Abu Hureyra was already an established sedentary community, and modifications to subsistence strategies, including cultivation, are suggested as a response to the decline of key plant resources in the local catchment (Moore and Hillman, 1992, Hillman et al., 2001). Bar-Yosef (2001, 2011) also discusses the impetus for cultivation in response to climatic pressures with reference to the Younger Dryas. He proposes that the knock-on effect of the climatic deterioration associated with the Younger Dryas led to the temporary retraction of the steppic belt (with attendant wild progenitors), which in turn may have driven 'demographic' pressures within the Natufian populations that occupied the Levant. Bar-Yosef (2011) suggests that responses may include activities associated with resource intensification (such as maintaining wild plant stands or cultivation), which paved the way for domestication.

Changes in the exploitation of plant resources due to unfavourable climatic conditions during the Late Epipalaeolithic have been challenged; the cold and arid conditions of the Younger Dryas may not have exerted a major impact on a micro-ecological scale, in terms of the availability of certain food resources and settlement activity, certainly in the core area of the Early Natufian group (Willcox, 2005, 2007, Willcox et al., 2009, Maher et al., 2011, p. 21). For instance, Abbo et al. (2010b) cite Halstead's (1989) concept of 'normal surplus' and the need for farming communities to generate sufficient surplus to cover drought years to achieve a sustainable economy, which requires climatic conditions with good rainy years. On this basis, Abbo et al. (2010b) suggest that persistent deterioration in climatic conditions (such as those of the Younger Dryas) are more likely to prompt mobile lifeways and migration to more resource-rich locations, rather than intensification strategies in resource-depleted locations. Indeed, Bar-Yosef (2001, 2011) himself acknowledges that during periods of climatic instability and deterioration, Late Epipalaeolithic communities may have adopted other strategies such as increased (seasonal) mobility in areas that were not resource-rich, or asserting ownership of resource-rich locations, as well as resource intensification strategies. Abbo et al. (2010b) also refer to Diamond's (2005, pp. 423-426) concept of 'creeping normalcy' in terms of the amplitude of changes in climatic conditions (such as the Younger Dryas) as experienced in the lifespan of hunter-gatherer groups, and how this may not have been acute enough to prompt change and innovation in subsistence strategies (i.e. resource intensification and domestication). Another argument against the emergence of farming in response to the unfavourable conditions of the Younger Dryas is that archaeological evidence for the first farming communities immediately follows the termination of the Younger Dryas (Colledge and Conolly, 2010). This is based on evidence relating to settlement size and patterns, and the presence of 'special' features interpreted as dedicated food processing areas or grain stores, such as the 'kitchen' at Jerf el Ahmar (Willcox, 2002).

There is a strong body of evidence indicating that reduced atmospheric carbon dioxide $(CO₂)$ was a global limiting factor for the process of domestication during the Late Pleistocene (e.g. Sage, 1995, Richerson et al., 2001, Cunniff et al., 2010, 2008, 2016). Sage (1995) uses Antarctic ice core evidence (Barnola et al., 1987, Neftel et al., 1988, Jouzel et al., 1993), in conjunction with a synthesis of CO₂ depletion and enrichment studies and analyses of plant functional traits, to propose that plant photosynthesis and productivity was significantly constrained under the reduced CO₂ conditions experienced during the Late Pleistocene. Richerson et al. (2001) also draw on studies of palaeoclimate data (including climate proxies from ice-cores, marine- and terrestrial-cores), to discuss how the climatic conditions during the Late Pleistocene (i.e. dry, low CO₂ and highly changeable) were not conducive to the development

of agriculture. Based on experimental research designed to test the CO₂ limitation hypothesis, Cunniff et al. (2008, 2010, 2016, 2017) confirmed that the increases in CO₂ levels from the late glacial to the early Holocene facilitated both direct and indirect physiological improvements. The increase in CO₂ level from 18 Pa to \sim 27 Pa would have allowed southwest Asian wild wheat and barley crop progenitors to allocate resources to reproductive rather than vegetative growth, which would improve their water status, germination rates and seed viability, resulting in higher grain yield per plant. Overall enhanced productivity of the wheat and barley progenitors due to the effects of increased $CO₂$ would have provided an increasingly stable food base (Cunniff et al., 2010, 2016), facilitating increased sedentism and potentially population increase (Cohen, 1977, Cunniff et al., 2010). Both Cunniff et al. (2010) and Sage (1995) therefore see favourable climatic conditions during the Holocene as a 'precondition' for successful agriculture rather than seeing agriculture as a response to the 'push' of deteriorating climate.

Demographic (population) pressures have been proposed as another push factor instigating the deliberate domestication of plants (e.g. Binford, 1968, Cohen, 1977, 2009). A model developed by Binford (1968) focuses on the fringes of the resource-rich habitats of southwest Asia, often termed the "Marginal Zones", which he viewed as important for emergence of domestication in the post-Pleistocene period. The model hinges on population-resource imbalance as an impetus for cultivation, whereby following the improved conditions associated with the termination of the Pleistocene, increased sedentism and population growth within resource-rich (optimal) environments in the Levantine Corridor forced population expansion into regions with lower carrying capacity (Binford, 1968). Binford (1968) proposed that resource intensification strategies (including cultivation) were adaptations in response to changes in the population/resource equilibrium. Cohen (2009, p. 591), on the other hand, suggests that post Pleistocene increases in population, a "supraregional" factor, led to relatively synchronous domestication events in different parts of the world. Cohen (1977, 2009) asserts that the domestication of plants was an intentional response to mitigate resource depletion, caused by an imbalance between population demand and availability of food resources. He later concedes that this model is not contingent on change or innovation due to population growth alone, but that social or political factors may have contributed to pressure on resources (Cohen, 2009).

Garrard et al. (1996), however, refuted Binford's (1968) marginal zone model as the impetus towards domestication, due to the lack of direct evidence for the domestication of plants or animals from Epipalaeolithic or Early Neolithic sites, in what is now dry steppe and sub-desert belt ('Marginal Zone') to the east and south of the Levantine Corridor. Population pressure

models for the emergence of agriculture, such as Cohen's (1977), have been criticised on the grounds that identifying evidence for population pressure in the archaeological record is difficult, as is determining what may be perceived as food shortages (Cowgill, 1979, Winterhalder and Kennett, 2006, p. 5). Estimating population size based on settlement patterns may provide some insight into population pressures (Price and Bar-Yosef, 2011), and large populations are inferred from the "megasite" village phenomenon associated with Late Pre-Pottery Neolithic at sites such as 'Ain Ghazal, es-Sifiya, and Basta in Jordan (Belfer-Cohen and Goring-Morris, 2011). Agriculture also emerged during the Late Pre-Pottery Neolithic (Zohary et al., 2012), but Cohen (1977) discusses demographic pressures and the development of agriculture around the end of the Pleistocene. Furthermore, pressures associated with population growth during the Late Epipalaeolithic and Early Neolithic periods may have been experienced at regional scales rather than universally across the Fertile Crescent, depending on the resource-capacity of the settlement locations and societal responses to population growth (Belfer-Cohen and Goring-Morris, 2011).

Other researchers (e.g. Bender, 1978, Hayden, 2009, Hayden et al., 2013) advocate explanations for the emergence of domestication that focus on internal socio-cultural pressures ('pull' models), as opposed to external pressures (climate or resource depletion). Bender (1978) stresses that hunter-gatherer communities' responses to external pressures (notably climate and population) and the emergence of agriculture are both contingent on social factors. She proposes that agriculture may have emerged through the generation of surplus to cover social obligations (such as reciprocity to cover immediate shortfalls in foods, or wider marriages/alliances) that ensure the survival of hunter-gatherer groups (Bender, 1978). These reciprocal situations would lead to increased demand for food and the potential development of resource intensification strategies, such as cultivation (Bender, 1978). Hayden (1990, 2009, 2010, 2014, Hayden et al., 2013) is another advocate of the potential role that the generation of surplus played in the origins of agriculture. He argues that feasting was an important facet of semi-sedentary hunter-gatherer societies. Activities such as feasting can promote social cohesion, but can also permit 'self-promotion' and increase social status through competitive feasting (Hayden, 1990, 2009, Hayden et al., 2013). Feasting entails the need to create a food surplus (Hayden, 1990, 2009, 2010), and the process of domestication may be borne out of the demand for desirable (e.g. high calorie) food items, such as cultivars, for feasting and the production of 'special' foods like beer and bread (Dietrich et al., 2012, Hayden et al., 2013, 2016, Arranz-Otaegui et al., 2018). These economic demands could be met through intensification of resource acquisition (Hayden, 2009). These socio-cultural pull models, therefore, depend on the ability and impetus to generate food surplus.

The concept of food surplus and what constitutes surplus for a given society or time period is not straight forward (Bogaard, 2017). Determining what is 'enough' is dependent on the 'mindset' of a particular group, which is shaped by cultural and socio-political parameters, and not simply by biological need for the maintenance of the primary unit of production (Hastorf and Foxhall, 2017). Crop surplus, whether for seed stock, to cover crop failure and/or as a commodity, also requires storage. A consideration of storage has been used to criticise theories that focus on the importance of the production of a surplus as a driving force for the development of agriculture (such as Bender, 1978, Hayden, 1990, Hayden et al., 2013). For instance, identifying primary evidence for storage (such as storage containers or other storage features) is problematic, especially at Late Epipalaeolithic and Early Neolithic sites, as the types of materials used to store surplus may not be visible in archaeological record (see Kuijt, 2009). In addition, direct archaeological evidence for feasting during these periods is often ambiguous, as is the role of plant products (like bread or beer) in such activities (Twiss 2008, Kuijt, 2009). It is therefore difficult to gauge if, and to what extent, surplus may be been generated and stored during the pre-/early domestication periods in southwest Asia (Twiss, 2008, Kuijt, 2009, Hastorf and Foxhall, 2017), and therefore to determine the significance of surplus as a principal driving force in the process of plant domestication. In addition, Kuijt (2009) questions Hayden's (1990, 2010) idea of 'competitive' feasting, arguing that in the early stages of plant domestication, there is limited evidence for social differentiation in the Late Epipalaeolithic and earliest Neolithic communities of southwest Asia (Kuijt, 1996).

Most of the explanations for the emergence of agriculture described above involve conscious decisions on the part of hunter-gatherer communities, but there is also a long history of thought that considers that domestication arose from unintended (or unconscious) selection pressures without an intention to modify (or domesticate) the wild species. The term "unconscious selection" was first coined by Darwin (1959) in the $19th$ century and subsequently taken up by later proponents of this idea (e.g. Darlington, 1963, Harlan et al., 1973, Heiser, 1988, Zohary, 2004) who argue that domestication arose from unintentional selection pressures within the anthropogenic environment. Archaeological evidence (in particular faunal remains) suggesting a diversification in the diet during the Upper Palaeolithic led Flannery (1969) to develop the concept of the 'Broad Spectrum Revolution' (BSR). He proposed that diversification strategies that incorporated more fish, small game, waterfowl and herbaceous plants (including wild cereals and pulses) into the diet occurred as a response to resource depletion, though he rejects the idea that this change was a direct result of environmental change (Flannery, 1969). Instead, he favoured Binford's 'disturbed density equilibrium' model, occurring in marginal areas receiving overflow from an expanding population in resource-rich

areas. He saw this broad spectrum as "setting the scene" for domestication, and suggested that agriculture arose not in the optimal areas where wild cereals were abundant, but in these more marginal areas, in an attempt to replicate artificially the dense cereal stands of the optimal zone (Flannery, 1969).

Optimal foraging theory, and in particular the diet breadth model, has been used to explain the apparent switch to the exploitation of a broad spectrum of food resources in the Upper Palaeolithic. This explanation hinges on foragers' responses to changes in resource availability, whether induced by environmental conditions or population pressure, and how they attempt to maximise the benefits obtained per unit foraging time, which results in the greatest possible (optimal) benefit to their survival and reproductive success (Smith, 1983). The diet breadth model, centres on the ranking of species in terms of calorific value and input of time and energy to acquire the resources (cost benefit analysis) (Winterhalder and Goland, 1997, Stiner et al., 2000, Stiner, 2001, Stiner and Munro, 2002), rather than species taxonomic diversity alone (Stiner et al., 2000). An important aspect of the diet breadth model is that foraging will always be pursued on an encounter basis, and that ignoring a potential (lower-ranked) food resource reduces overall foraging efficiency (Gremillion and Piperno, 2009). Winterhalder and Goland (1997) highlight the fact that even 'low-ranked' resources such as small seeds can achieve considerable dietary important if they occur in high densities. Moreover, the chances of encounter increase with density, and frequent encounters result in frequent use, this potentially paving the way to domestication (Gremillion and Piperno, 2009). It would therefore follow that, in times of resource stress (such as climatic deterioration or population increase), a broader spectrum of foods will be exploited, including lower-ranking species, such as small animals and wild grasses (Stiner et al., 2000, Stiner, 2001, Stiner and Munro, 2002, Winterhalder and Kennett, 2006).

Nevertheless, the diet breadth hypothesis as an explanation of the broad spectrum of resources exploited un the Upper Palaeolithic (Winterhalder and Goland, 1997, Stiner et al., 2000, Stiner, 2001, Stiner and Munro, 2002, Winterhalder and Kennett, 2006, Gremillion and Piperno, 2009, Gremillion et al., 2014) has been challenged. For example, the benefits of encountering high-density wild grass stands and the ease of gathering may be negated by the labour-intensive, processing costs of wild grasses (Wright, 1994). This is primarily attributed to the fact that processing grasses for consumption (such as by threshing and grinding) to make them edible is very labour intensive (Wright, 1994, Hayden et al., 2016, Arranz-Otaegui et al., 2018) and, as such, grasses tend to be considered an emergency foodstuff amongst traditional hunter-gatherer groups (Wright, 1994). Smith (2011a) and Zeder (2012a, 2014) have criticised the optimal foraging theory as an explanation for the switch to a broad spectrum of food

resources, because they only relate to foraging strategies under circumstances of resource depression, whereas the archaeological evidence suggests the emergence of a broad spectrum taking place under resource-rich, stable conditions (e.g. Sage, 1995, Gupta, 2004, Bettinger et al., 2009, Willcox et al., 2009, Cunniff et al., 2008, 2010, 2016, Abbo et al., 2010b, Zeder, 2012a).

Unlike the 'push/pull' models discussed above, optimal foraging theory (the diet breadth model) does not depend on a deliberate decision to domesticate plants and, indeed, the theory is primarily used to explain the exploitation of a broad spectrum of wild foods rather than domestication *per se*. It does however, rely on resource depletion as a stimulus to changing resource exploitation, so has elements in common with theories based on environmental deterioration or population expansion. Other approaches emphasise the selection pressures acting on wild plants once they had been removed from their natural environment to that of a managed man-made environment (Darlington, 1963, Harlan et al., 1973, Heiser, 1988, Zohary, 2004). It is argued that the expression of many of the traits that characterise crops and distinguish them from their wild ancestors (i.e. traits including, but not limited to, non-shattering, free germination, increased seed size, synchronous tillering), arose from the repetitive cycle of sowing, harvesting and re-seeding of stored seed stock (Darlington, 1963, Harlan et al., 1973, Hillman and Davies, 1990). Harlan (1973, p. 321) also proposed that this process of unconscious selection could be reinforced by conscious selection, whereby deliberate human selection pressures (such as choosing harvested seed for sowing subsequent crops) were 'superimposed' on the automatic selection pressures. Heiser (1988) and Zohary (2004) also support the concept of unconscious selection, with the planting of seed and the conditions of cultivation being critical factors in the process of plant domestication.

Others take this further by suggesting that domestication began even before cultivation when Early Neolithic sedentary communities inadvertently created a new environmental niche due to accumulation of domestic debris, resulting in fertile disturbed environments in the immediate environs of the settlement that potentially favoured ruderal (weedy) species. This led to explanations of early plant domestication models such as the 'dump-heap' hypothesis (first proposed by Engelbrecht, 1916, see also Zeven, 1973), whereby domesticated species would have evolved from species growing in the disturbed and fertile conditions associated with habitation (see Abbo et al., 2005 for further discussion). Such dump-heap models (e.g. Sauer, 1952, Harlan, 1965, Harris, 1969, Hawkes, 1969) have been contested on ecological grounds (Blumler, 1996, Abbo et al., 2005, 2009, 2011a, Zeder, 2015). Legumes (which are nitrogen-fixing), they argue, would not thrive on such nutrient-rich soils and wild cereals are relatively late colonisers of disturbed areas compared to other (genuine) ruderal species, such

as *Urtica* spp. (nettles) or wind-blown Compositae (dandelion-type) (Blumler, 1996, p. 39, Abbo et al., 2005, p. 493). Blumler (1996, p. 33) also points out that wild grasses require little, if any, disturbance to thrive in abundance and questions whether the amount of harvestable produce from such soils would draw enough interest to prompt further propagation of wild cereals. There is acknowledgment that, despite being a poor competitor as a colonising species, under managed conditions (i.e. under cultivation) wild cereals could have an advantage over other wild species (Blumler 1996, p. 34).

Rindos (1980) offered a model that views the process of plant domestication based on a dynamic mutualistic relationship between some plant species and humans, whereby their interrelationship enhances both parties' ability to thrive. He proposes that those species that adapted and thrived under the anthropogenic conditions became domesticated, independently of whether there was deliberate intent on the part of the cultivator (Rindos, 1980, 1984). Rindos (1980) also contends that the management and manipulation of local environments to improve or alleviate the ecological constraints of the natural environment created new ecological niches that favoured some species. For example, woodland clearance to create more open habitats, whether for grazing, habitation or cultivation, would result in favourable conditions for certain wild herbaceous species (the crop progenitors) that thrive in such habitats (Rindos, 1980). He argues that these species entered into a mutualistic relationship with people, to the exclusion of other previously collected species, resulting in the selection of adaptive domestication traits in the progenitor species, while human populations became increasingly dependent on this smaller number of species (Rindos, 1980, 1984). Rindos' (1980, 1984) model has been criticised for seemingly being orthogenetic (i.e. evolution along a single ecological continuum), implying that there was natural and inevitable sequence for the process of domestication (foraging, domestication, agriculture), thereby side-lining the influence of human behaviours (e.g. Zeder and Smith, 2009, Abbo and Gopher, 2017). Rindos (1980, p. 769) does acknowledge that his model may be read as implying orthogenesis, but refutes this as misinterpretation of his model. Blumler (1996) has also questioned Rindos' (1980) claims of the natural 'weedy' tendency of progenitors as early colonisers of disturbed/cleared ground, which is a trait that Rindos cites as a reason why wild progenitors were successful candidates for domestication in anthropogenic habitats.

Other models that use niche construction theory (Day et al., 2003, Laland and O'Brien, 2010), such as woodland clearance, also view the process of domestication as a dynamic mutualistic relationship between plant and humans, but consider conscious selection to be an essential factor in the domestication process (e.g. Smith, 2007, 2011a, 2011b, 2015, 2016, Zeder and Smith, 2009, Zeder, 2011, 2012a, 2015, 2016). During the early phases of low-level food

production (see Smith, 2001), protagonists of niche construction theory place emphasis on plant 'management' activities and niche construction behaviours in resource-rich environments (Smith, 2007, 2011a, 2016, Zeder and Smith, 2009, Zeder, 2012, 2015). Such niche construction behaviours entail the manipulation of the growth conditions of an organism or the environment that sustains it, wherein the conditions are deliberately engineered in order to increase its relative abundance and predictability, and simultaneously reduce the time and energy needed to harvest it (Smith, 2011b, 2015, Zeder, 2015). For instance, niche construction behaviours may include maintaining stands of economically valued plants by removing competitors for nutrients, sunlight and soil moisture or increasing stand abundance by sowing seeds in areas of cleared ground (Smith, 2011b). Zeder (2015, p. 2) acknowledges that such plant management strategies do not necessarily lead to domestication. Both Rindos and niche construction proponents recognise that domestication is only likely if the selection pressures on the managed resources are sufficiently different from those experienced in natural habitats, or are maintained over several generations, and if the adaptations to growth in a managed environment are of positive benefit to both plants and humans (Rindos, 1980, Zeder, 2015).

Gremillion et al. (2014, p. 6175) suggest that the explanatory power for understanding the process of domestication provided by niche construction theories is constrained, because they do not adequately address why humans alter their resource acquisition patterns (e.g. unlike models based in optimal foraging theories, where the impetus for change lies in demand/resource imbalance). Abbo and Gopher (2017, pp. 504-506), staunch supporters of the importance of conscious selection pressures, have also argued that models that adopt niche construction theory minimise the role of human decision making in the process of domestication, who appear as passive or near-equal partners in such coevolutionary relationships. They attribute the side-lining of human agency in certain models for the emergence of agriculture (such as niche constuction theory) to gaps in the various disciplines that focus on plant domestication, for example biologists (and archaeobotanists) not closely incorporating sociocultural considerations in their models (Abbo and Gopher, 2017, p. 504).

1.3.2 The role of plant traits in explanations for the process of plant domestication

On the basis of experimental evidence, Hillman and Davies (1990) suggested that the harvesting of wild grasses may have acted as an inadvertent filter selecting non-shattering dispersal units. They harvested wild cereals by three methods: beating spikelets into baskets, uprooting plants and cutting stems using sickles. Their results indicated that uprooting or sickle

harvesting of partially or near ripe wild cereals selected for the greater retention of nonshattering dispersal types over shattering types, the latter being more prone to being dispersed in the process of collecting (Hillman and Davies, 1990). If the collected grain were retained and re-sown in virgin land, this would have resulted in an increase of non-shattering types on the re-sown land (Hillman and Davies, 1990). If this inadvertent selection for nonshattering types were repeated in future years, then the crop would become predominantly of the non-shattering domesticated type. Whilst being an advocate of unconscious selection generally, Fuller (2007, pp. 920-921) points out that there is archaeological evidence for the use of sickles long before the appearance of domesticated cereals, and argues that it was only much later (well after domestication) that sickles were used to harvest cereals. Therefore, as sickles are a feature of the Natufian and PPNA tool kit, using the Hillman and Davies (1990) model for the selection of non-shattering rachis as driven by sickle harvesting, the appearance of domesticated (non-shattering) cereals would be expected to appear earlier than the PPNB (Fuller, 2007).

Microwear analysis (the degree of polish and striation patterns) of sickle blades from Natufian and Early Neolithic sites has been compared with microwear patterns of lithic tools used in experimental harvests of wild cereals (Anderson, 1992, 1998, Ibáñez et al., 1998). Changes in the polish and striation patterns of sickle blades (decreased polish and more uniform striation microwear patterns) associated with early agrarian sites, such as Abu Hureyra, Mureybet and Tell Halula, are taken to reflect the harvesting of ripe stems of domesticated cereals. Conversely, more polished and more varied striation patterns on sickle blades tends to be associated with pre-agrarian lithic assemblages and indicates harvesting of green or semigreen stems of wild cereals (or other wild grasses), a strategy that would limit the loss of grain through the disarticulation of ripe (shattering type) spikelets (Anderson, 1992, 1998, Ibanez et al., 1998). More recently, Maeda et al. (2016) found no strong correlation between percentages of cereals and sickle blades at sites in the Fertile Crescent, and on this basis, both Fuller (2007) and Maeda et al. (2016) argue that sickle harvesting of wild cereals was not the driving force selecting for non-shattering rachis.

Based on ethnographic studies of post-harvest processing in Turkey, Hillman (1984) also suggests that grain sieving to remove weeds etc. would have inadvertently removed 'tail grain' (the smaller grains that pass through the sieve) resulting in the selection of large grains. Doubt has been cast on sieving as a selection pressure for large grain size, however, as the large grain is still from the same genetic stock as the small tail grain (Fuller, 2007, p. 909). Depth of seed burial has also been proposed as a mechanism for unconscious selection for large seed size, as the deliberate act of planting seeds would have buried them at a greater depth than would
happen through natural mechanisms (Harlan et al., 1973, Zohary, 2004, Fuller, 2007), which potentially favoured larger seeds (Fuller, 2007, p. 909). Kluyver et al. (2013) tested this theory through growth experiments on pulses, recording how long it took seeds buried at different depths to emerge above ground, and their results show that deep burial does not necessarily select for larger seeds in wild or domesticated pulses.

Another trait associated with domestication is loss of seed dormancy (Harlan et al., 1973, Fuller, 2007). Both wild cereals and wild pulses exhibit seed dormancy, although it is much higher in wild pulses (~85-90%) compared to wild cereals (~50%) due to their hard, impermeable seed coats (Ladizinsky, 1987, Zohary, 1989, Abbo et al., 2009, 2011b). Low germination rates in wild lentil (~10%) led Ladizinsky (1987) to argue that it was not suitable for cultivation without loss of seed dormancy, and that this might very likely be the case for other wild pulses. He theorised that loss of seed dormancy in pulses evolved before cultivation; using mathematical models of gene mutation rates for loss of dormancy in wild lentil, he sought to demonstrate that the consistent and massive harvesting of wild lentil seed by hunter-gatherers would have led to fixation of genes that confer non-dormancy in natural populations after seven years (Ladizinsky, 1987). Ladizinsky's (1987) theory for the precultivation domestication of lentil has been criticized by Zohary (1989) and Blumler (1991b), because the model does not account for year-to-year yield variability of wild lentil (the model is based on a constant yield assumption of 10 seeds per plant) or for a pre-existing soil seed bank of dormant wild lentil. The mass removal of fresh seed, which is an important factor in Ladizinsky's (1987) model, is also not contingent on harvesting by hunter-gatherers, but may also occur through predation from grazing pressures or weather conditions, which may result in the same rate of mutation for the fixation of the non-dormant allele (Zohary, 1989, Blumler, 1991b). Instead, it is argued that seed dormancy in wild lentil is more likely to break under cultivation, whereby non-dormant seeds would tend to have a greater contribution to the harvested crop due to their higher germination rate, leading to their increased importance over time. Both authors, therefore, propose that loss of seed dormancy arose after wild pulses had been brought into cultivation, and refute Ladizinsky's (1987) hypothesis that loss of seed dormancy in wild lentil evolved prior to cultivation (Zohary, 1989, Blumler, 1991b).

It has also been suggested that there may be differences in the pathways to domestication between cereals and pulses, and that pulses (at least) became domesticated because of deliberate (conscious) human selection (e.g. Abbo et al. 2009, 2011b). The differences between cereals and pulses, in their growth habit and habitat preference have been discussed by Abbo et al. (2009), and are summarised in Table 1.1. Typically, wild cereals are encountered in greater frequency and density than wild pulses, which have patchy distribution with sparse

populations, and produce greater yields (200g-over 1kg seed harvested per hour) than wild pulses (less than 100g seed harvested per hour) (Abbo et al., 2008b, Abbo et al., 2009). Abbo et al. (2009, 2011b) maintain that, for pulses in particular to be domesticated (due to high rates of seed dormancy and low, sporadic yields of wild pulses compared to wild cereals), it was necessary for early cultivators to have an understanding of wild pulse morphological and physiological traits, as well as desire to cultivate these species (Abbo et al., 2009, 2011b). Without this understanding of plant species biology and a motive to cultivate wild pulses, advocates for human agency maintain that it would not have been possible to overcome issues of high rates of seed dormancy and low yield returns under cultivation, compared to what yields could be foraged from naturally distributed populations (Abbo et al., 2009, 2011b). Abbo et al. provide support for these arguments for conscious selection and pulse domestication, based on their growth and harvesting experiments of wild pea, chickpea and lentil, both from experimental plots and harvesting plants in their natural habitats in Israel, which demonstrate the low and sporadic yield of wild pulses, as well as no net yield return for the cultivation of wild pea (Abbo et al., 2008a, 2008b, 2009, 2011b, 2013b). Accordingly, those that support models for a rapid process of domestication (particularly in the case of pulses) are also those that favour models based on conscious selection, since it seems unlikely that the cultivation of wild species that result in no economic gain would be sustained over several centuries or millennia (Abbo et al., 2009, 2011b, 2013).

Blumler (1991b) suggests that wild pulses might have been deliberately brought into cultivation to avoid scheduling conflicts between foraging for wild pulses and cereals. In these circumstances, hunter-gatherers might have abandoned the exploitation of wild pulses, which are patchy and sporadic in distribution, and deliberately selected them for cultivation near wild cereals, under which conditions the rapid selection for non-dormancy of seed and gradual selection for pod indehiscence arose, which ultimately led to pulse domestication (Blumler, 1991b). There is some agreement with those scholars that tend to favour unconscious selection that loss of dormancy and pod indehiscence are likely to have occurred early on in the process of pulse domestication, under conditions of cultivation, and that the process of pulse domestication may have been faster than that of cereals (e.g. Fuller, 2007). Willcox et al. (2009) also suggest that the increase in use of pulses at Early Neolithic sites in northern Syria (such as Jerf el Ahmar, Tell 'Abr, Mureybet III, Dja'de and Halula) may be linked to the adoption of cultivation, due to the sparse distribution of wild pulses in natural habitats making gathering on a large scale difficult.

1.4 Functional Ecology as an approach to understanding plant domestication

1.4.1 Introduction

The traditional approach to identifying evidence for plant domestication, based on the morphology of ancient plant remains, is limited to identifying whether they are remains of crops, crop progenitors or wild species. This morphological approach will not enable insight into the selective pressures that led particular species to become domesticated. Functional ecology, applied to extant plants, lends itself well to the investigation of plant domestication by identifying domestication traits that cannot be directly observed in the archaeobotanical record. More specifically, it enables the identification of functional traits that distinguish crop species and their wild progenitors from other wild species that were collected by early huntergatherers but not domesticated. Based on these functional traits, it is possible to explore the selective pressures that were acting on wild plants and progenitors, as well as the changes that occurred when wild progenitors became domesticated crops.

Functional ecology was borne out of the quest of plant ecologists to find general rules linking species, biodiversity, ecosystem functioning and environmental gradients (Calow, 1987, Keddy, 1992, Albert et al., 2011). The purpose of functional ecology is to describe species by their biological characteristics through the measurement of functional traits (Albert et al., 2011), which are heritable plant features that are measurable at the individual level, from cell to whole organism, and contribute to fitness (Violle et al., 2007, Garnier et al., 2016). These plant features, or functional traits, are the product of evolutionary and community assembly processes (i.e. processes that influence the identity and abundance of species in ecological communities (Kraft and Ackerly, 2014, p. 68)) in response to abiotic and biotic environmental constraints (Valladares et al., 2007, Kattge et al., 2011). Functional traits determine how plants respond to environmental factors, affect other trophic levels and influence ecosystem properties (Kattage et al., 2011). This approach can be used at different scales (individual, community, ecosystem and biome), making it a useful investigative tool for answering a wide range of ecological questions.

Over the past twenty years, the functional ecological approach has been successfully applied to archaeobotanical research questions. It has been applied, for example, to crop weed assemblages to identify past crop husbandry practices and so improve our understanding of the nature and social significance of farming practices in Europe and western Asia (see Section 1.4.3). More recently, archaeobotanists and evolutionary ecologists have collaborated in order

to address questions relating to the process of plant domestication using a functional ecological approach (see section 1.4.3.2).

1.4.2 Principles of functional ecology

Ecosystems are driven by the functional traits of individuals, their distribution and abundance, and their biological activity (Naeem and Wright, 2003). Within ecology, 'function' refers to a specific activity that is performed at different organisational levels in the living world, for example (in the context of this thesis), specific activities that are performed by plant cells, plant organs or the whole individual (Garnier et al., 2016, p. 3). The definition of what a functional trait is has developed over recent years, from a Darwinian meaning as a 'proxy' for 'organisational performance' (within different levels of organisation including the individual, population, community and ecosystem) to a more ecologically explicit definition as 'any morphological, physiological, or phenological feature measurable at the individual level, irrespective of the environment or level of organisation' (Violle et al., 2007, p. 884). A distinction is made between performance traits (e.g. vegetative biomass, reproductive output, plant survival), which contribute directly to fitness, and functional traits, which are the morphological, physiological or phenological traits that have an impact on performance traits (and therefore contribute indirectly to fitness) (Violle et al., 2007). The attribute of a functional trait is the value (measurement) of that trait, usually based on the average value of the attributes of several individuals within a population (Violle et al., 2007). This is because within a species, a trait may have different attributes (values) on an environmental gradient, such as temperature, moisture or soil chemistry, and therefore it is usual for a trait to represent a population, rather than the entire species (McGill et al., 2006, Violle et al., 2007, see also Cornelissen et al., 2003, Perez-Harguindeguy et al., 2013).

Functional classifications are also a good tool for the simplification of floristic complexity in small-scale community ecological models through to global vegetation models (past, present and future) (Lavorel et al., 2007). The functional trait-based approach enables the generation of generalised and predictive ecological models, unlike those that are based on a nomenclatural approach, which focus on species identities (Keddy, 1992, McGill et al., 2006). Another significant advantage of functional ecology is the use of easy-to-measure traits (also known as 'soft' traits, such as specific leaf area), which are proxies for hard-to-measure functional traits (i.e. 'hard' traits, such as growth rate) that require more labour-intensive, time-consuming, and often expensive methods required to obtain direct measurements of plant fitness (Hodgson et al., 1999, Weiher et al., 1999, Cornelissen et al., 2003, Perez-Harguindeguy et al., 2013). There have been concerted efforts to compile, and make available,

information on soft traits for large numbers of species from all types of vegetation (e.g. Díaz et al., 2004, Wright et al., 2004, Kleyer et al., 2008, Kattge et al., 2011, Kew, 2019). Through the exploration and application of these large trait datasets, a consensus has developed regarding which soft traits are most useful for representing key plant functions, such as resource conservation or acquisition, and how these traits translate to responses to climate and disturbance (Grime et al., 1997, Westoby et al., 2002, Westoby and Wright, 2006, Hodgson et al., 2011). This process of mass trait-data accumulation has also necessitated standardised field and laboratory methodologies, notably those of Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013).

The functional ecological approach was developed through the "Functional Interpretation of Botanical Surveys" (FIBS) project at the Unit of Comparative Plant Ecology (UCPE), Sheffield as a method for investigating the role of ecological processes in determining species distribution within a wide range of habitats (Hodgson, 1989, 1990, 1991, Hodgson and Grime, 1990). This approach built on a body of evidence, which indicates that there is a tendency for species tolerant of a particular ecological factor to share a suite of common adaptive characteristics i.e. to be of a particular "functional type"- and that other environments will engender different suites of attributes that characterise different functional types (Grime, 1979, Pugh, 1980, Reich et al., 1992). Functional types are therefore sets of plants that exhibit similar responses to environmental conditions (Walker, 1992, see also Noble and Slatyer, 1980, Díaz and Cabido, 1997, Grime, 2006). Plant functional types are useful for predicting ecosystem response to human- or climate-induced changes at a global scale, as they bridge the gap between plant physiology, and community or ecosystem processes (Díaz & Cabido, 1997). Functional ecology has been used to investigate a wide range of ecological issues, such as community ecology (Grime, 2006), responses to disturbance (Lavorel et al., 1997, Kleyer, 1999), including fire disturbance (Noble and Slatyer, 1980, Bond et al., 2005), the effects of climate (Prentice et al., 1992, Díaz and Cabido, 1997), including palaeoclimate (Prentice et al., 2000), and human impact on ecosystems (Osborne et al., 2018). In the following section, the use of functional ecological principles to address archaeological research questions will be discussed.

1.4.3 Application of functional ecology to archaeobotanical questions

1.4.3.1 Background

Plant ecological applications to archaeological research questions have primarily been concerned with the identification of ancient crop husbandry practices, through a study of weed seeds found in association with ancient cereal remains (see, for example, Knörzer, 1971,

Willerding, 1978, Wasylikowa, 1981, Jones, 1992, van der Veen, 1992). The weed species growing alongside crops reflect the environmental conditions in the cultivated field, which in turn reflect the agricultural practices applied to the crops with which the weeds grew (e.g. van der Veen, 1992, Jones, 1992, Jones, 2002). The species composition of these crop weed assemblages may, therefore, be used to identify past agricultural practices, and a variety of ecological approaches has been adopted for their interpretation in these terms. Most notable amongst these are the phytosociology of plant communities (synecology) (e.g. Braun-Blanquet, 1936, Tüxen, 1950), and the autecological habitat preferences of individual species (e.g. Ellenberg, 1950, Ellenberg, 1979). A limitation of most of these ecological approaches, however, is that they are based primarily on field observations and, as such, provide information about where a species grows, but not why it grows there (Jones, 2002). Functional autecology, on the other hand, provides a causal link that can be used to identify the selective pressures acting on plants under cultivation due to the agricultural practices applied.

Two collaborative research programmes on the functional interpretation of weed floras in relation to past crop husbandry practices (Charles et al., 1997, Jones et al., 2005, Jones et al., 2010) compiled a corpus of trait measurements, based on present-day representatives of archaeologically attested species in modern floristic surveys. These projects measured a range of functional attributes for weed species associated with crops grown under various contrasting cultivation regimes (such as irrigated and dry-farmed fields, intensive garden plots and extensive field systems) in different climatic regions and, from this body of data, it was possible to distinguish plant functional types that reflect the growing conditions under these different cultivation regimes. This functional ecological approach has been used successfully to distinguish between irrigated and dry-farmed cereals in the Borja region of Spain (Charles et al., 1997) and the Kerak region of Jordan (Charles et al., 2003), crop rotation and fallowing regimes in northern Jordan (Bogaard et al., 1999), crop sowing times in central Europe (Bogaard et al., 2001), intensive and extensive cultivation of pulses in Evvia, Greece (Jones et al., 2000a), and of cereals in Asturias, Spain (Charles et al., 2002), Haute Provence, France (Bogaard et al., 2016a), and Morocco (Bogaard et al., 2016b). The functional types identified in these surveys have then been applied to archaeobotanical material, by measuring the same functional attributes on modern specimens of weed species represented in ancient crop-weed assemblages, and comparing these with the present-day functional types, in order to identify past husbandry practices, such as irrigation, sowing time and intensity of cultivation (Bogaard, 2004, Bogaard et al., 2011, 2016a, 2016b, 2017, Jones et al., 2010).

1.4.3.2 Functional ecology and plant domestication

The use of functional ecology to gain a better understanding of plant domestication differs from other approaches in that it seeks to understand the selective pressures exerted on wild plants and early crop progenitors due to external factors such as climate and human manipulations of the environment. In this way, it is possible to identify the factors that drove the selection of particular wild species as potential domesticates, and factors that drove the evolutionary changes from progenitor to domesticate, through a comparison of the functional attributes of domesticated species, their wild progenitors and other wild species potentially collected by early hunter-gatherers but not domesticated. This approach is analogous to the use of behavioural ecology to understand the selective pressures acting on wild animal species during the process of animal domestication, whereby the behavioural characteristics of livestock progenitors are compared with those of other wild species that were hunted but not domesticated (e.g. Hale, 1969, Garrard, 1984, Price, 1999, Smith, 2007, Zeder, 2012b).

Recent studies using the functional ecological approach are making significant contributions, such as providing corroborative evidence and greater insight in relation to Sage's (1995) atmospheric CO₂ limiting hypothesis as a global limiting factor for plant domestication during the Late Pleistocene (Cunniff, 2009, Cunniff et al., 2008, 2010, 2016, 2017). Cunniff and colleague's research primarily focusses on 'hard' functional traits (i.e. direct but hard to measure traits). The procurement of hard traits, which are usually physiological traits (Weiher et al., 1999), can be expensive, labour intensive and, under laboratory conditions, often places restrictions on the range of species that can be included in order to accommodate the required number of replicates for statistical purposes. The research presented in this thesis uses only 'soft' functional traits (i.e. indirect but easy to measure traits) that tend to be morphological or anatomical traits (Hodgson et al., 1999). It is therefore less restricted in the number of species that can be included, allowing the incorporation of a greater range of wild grass and legume species for comparison with crop progenitors and domesticates. This is important because archaeobotanical evidence indicates that a wide range of wild grasses (and legumes) was potentially exploited for consumption during the Late Epipalaeolithic and Early Neolithic periods (Weiss et al., 2004a, Wallace et al., 2019).

This thesis explores this line of research through analyses of the functional traits of plants growing in the natural environment, as well as plants grown under experimental conditions for the purposes of this thesis. It considers both cereals and pulses, wild grasses and legumes, focussing on soft functional traits in order to create a large database for analysis. The results of these analyses are then discussed alongside other recent research using functional ecology (both hard and soft traits) to address research questions relating to plant domestication (Milla

et al., 2013, 2014, 2018, Cunniff et al., 2014, Preece et al., 2015, 2017, 2018, Martin-Robles et al., 2018, see Milla et al., 2015).

1.5 Research aims and objectives

1.5.1 Research aims

This thesis aims to identify the selective pressures responsible for the physiological, morphological and community composition changes associated with plant domestication in southwest Asia, and so improve our understanding of the types of human activities and environmental conditions that led to the emergence of agriculture in this region.

1.5.2 Research objectives

To achieve these aims to the functional attributes of domesticated crops, their wild progenitors and other wild species that were not domesticated were measured, analysed and interpreted, with the following objectives:

Objectives relating to research design

- To determine whether there are any differences in functional attributes between plants growing in natural environments and plants grown under experimental conditions;
- To determine whether there are any differences in functional attributes due to the geographic location of the wild plant populations;
- To determine whether there are any differences in functional attributes due to unintended differences in experimental conditions;

Objectives relating to research questions

- To identify functional differences between cereals and pulses;
- To identify functional differences between crop progenitors and other wild species that were not domesticated;
- To identify functional differences between crop progenitors and domesticated species;
- To determine whether observed functional differences between domesticates, progenitors and other wild species also apply at Late Epipalaeolithic levels of atmospheric carbon dioxide;
- On the basis of this functional analysis, to re-evaluate alternative explanations for the process of domestication and the emergence of agriculture in southwest Asia.

1.6 Thesis structure

This thesis comprises a further five chapters: Chapter 2 is divided into three sections that present the environmental and archaeological background for the research, and ends with a review of how a functional ecological approach is suitable for the exploration of alternative explanations for the process of plant domestication in southwest Asia. Chapter 3 describes the research methodology, including the rationale for the choice of functional attributes and their measurement protocols, details of the field collections and growth experiments, and the methods of data analysis. The results of the analyses are presented in Chapter 4, and these results are discussed in relation to the process of cereal and pulse domestication in Chapter 5. Finally, the conclusions and recommendations for further work are presented in Chapter 6.

Chapter 2: Background

2.1 Introduction

This chapter aims to place in context the process of plant domestication and the emergence of agriculture, by presenting the environmental and archaeological background associated with the transition period from hunter-gatherer to early farming lifeways in southwest Asia. The present-day environment and palaeoenvironment of southwest Asia are discussed in Section 2.2, and the archaeological background in Section 2.3.

2.2 Environment of the Fertile Crescent

2.2.1 Introduction

In southwest Asia, the Fertile Crescent is a vast and geographically varied region that ranges from coastal areas in the west (including parts of Israel, Palestine, Lebanon, Syria and Turkey), and low-lying plains to the elevated regions of the Taurus and Zagros Mountain range of Turkey, Iraq and Iran, towards the east (Figure 2.1). The transition from food gathering during the Late Pleistocene, to food production in the early Holocene, in this region, coincides with major climatic changes (Table 2.1), which had a significant impact on plant exploitation. These climatic oscillations, associated with the last glacial termination, have been cited either as a major causal trigger for the origins of agriculture in southwest Asia (Moore and Hillman, 1992, Bar-Yosef, 2011) or as a constraint on the emergence of agriculture (Sage, 1995, Richerson et al., 2001, Willcox et al., 2009, Cunniff et al., 2008, 2010, 2016, 2017; see Chapter 1). In the following section, the environment of southwest Asia (focussing on the region encompassed by the Fertile Crescent) is outlined in order to place in context the climatic and ecological factors that may have influenced the process of plant exploitation and domestication during this transitional period.

2.2.2 Geological Background

The soils encountered in the Fertile Crescent vary significantly from west to east and from north to south (Figure 2.2). In broad terms, shallow, often gravelly Leptosols are predominantly associated with the Taurus-Zagros Mountain range, whilst the area of the southern Levant, which geographically encompasses southern Syria, Lebanon, Palestine, Israel and Jordan (Asouti and Fuller, 2011), is dominated by Calcisols and Luvisols. Calcisols contain secondary accumulations of lime and tend to be sparsely vegetated, being dominated by xerophytic shrubs and trees and/or ephemeral grasses (i.e. trees and shrubs adapted to

surviving in arid habitats and short-lived grasses), and are typically used for extensive grazing (FAO/IUSS/ISRIC, 2006, p. 74). Calcisols require careful irrigation for successful cultivation of crops such as winter wheat, and in some areas arable farming is impeded by stoniness of the surface soil and/or a petrocalcic horizon (FAO/IUSS/ISRIC, 2006, pp. 74-75). Petrocalcic horizons occur under conditions where calcium or other carbonates accumulate in the subsoil to the extent that the soil becomes cemented into hardpan (Bockheim, 2014, p. 109). Luvisols are characteristic of regions with distinct dry and wet seasons and are often quite fertile, but can be susceptible to erosion (FAO/IUSS/ISRIC, 2006). The eastern region of the Fertile Crescent, including parts of southern Turkey, Iraq and Iran, is characterized by soils that require careful water management in order to be agriculturally productive, particularly in the case of the strongly saline Solochak soils and the arid conditions associated with Gypsisols (FAO/IUSS/ISRIC, 2006). Fluvisols are also found associated with the Tigris-Euphrates river system, which flows south from the Taurus Mountains in southeast Turkey, through Syria and Iraq (Figure 2.1). These are often quite fertile, but again require some water management when under cultivation (FAO/IUSS/ISRIC, 2006).

2.2.3 Current Climate and Vegetation

2.2.3.1 Current climate of the Fertile Crescent

The climate of the Fertile Crescent is discussed here with reference to the Köppen-Geiger climate classification system, which is a world climate classification system based on five phytogeographic vegetation groups, and global datasets of high-resolution climate observations (see Kottek et al., 2006). The five vegetation groups and climate classifications used in the Köppen-Geiger system are developed from those determined by the French botanist de Candolle, based on climatic zones first defined by ancient Greeks (i.e. one torrid, two temperate and two frigid) (Sanderson, 1999, Kottek et al., 2006). The Köppen-Geiger system uses three letters to classify climates as follows: the first letters are used to distinguish plants from the equatorial zone (A), the arid zone (B), the warm temperate zone (C), the snow zone (D) and the polar zone (E) (Kottek et al., 2006, p. 259). The second and third letters of this classification system reflect the precipitation and temperature respectively (Kottek et al., 2006, p. 259, Peel et al., 2007, p. 1636), as shown in Figure 2.3. Today, the region of the Fertile Crescent falls within the arid and warm temperate zones, with some geographic variation (Kottek et al., 2006). Based on climate classifications using the Köppen-Geiger system (Peel et al., 2007, Figure 8), the Levant and the north-east and western fringes of the Fertile Crescent predominantly experience warm and temperate climates, with dry hot summers (Csa), where the monthly mean temperature for the hottest month is at least 22°C (Kottek et al., 2006). Areas of Syria, Jordan and Israel are subject to arid steppe climates, with some areas

experiencing hot (mean annual temperature of at least 18°C) or cold (mean annual temperature of <18°C) conditions (BSh and BSk respectively), which transition to hot arid desert climates (BWh) towards the western side of the Levantine Corridor (Figure 2.3). The eastern Fertile Crescent, including parts of Iraq and Iran, is characterised by hot arid steppe climates (BSh) at higher altitudes and hot arid desert climates at lower altitudes (BWh) (Figure 2.3), with the mean annual temperatures for these areas being at least 18°C (Kottek et al., 2006).

Air temperature is an important climatic parameter and is often used to assess regional climate variations and climate change. The region of the Fertile Crescent is strongly influenced by complex interactions between the mid-latitude Westerlies, the Siberian Anticyclone and the Indian Ocean Summer Monsoon (Sharifi et al., 2015). In the summer season, the mid-latitude westerlies are associated with warm air streaming in from the west (Harman, 1987), while the Indian Ocean Summer Monsoon brings warm, humid air from the southwest Indian ocean between April and September (Goswami and Chakravorty, 2017). The Siberian Anticyclone, also known as the 'Siberian high' (Hasanean et al., 2013), is associated with the coldest and densest air masses in the Northern Hemisphere (Cohen et al., 2001). In the winter season the Siberian Anticyclone dominates the majority of continental Asia (Gong and Ho, 2002, Hasanean et al., 2013), and therefore plays an important role in the climate of this region (Cohen et al., 2001, Hasanean et al., 2013).

Inter-regional climatic variation is apparent in the modern mean annual precipitation (MAP), with a significant west-east climate gradient across the Fertile Crescent (Figure 2.4), and today the Levant and the higher altitude (mountainous) regions of the Fertile Crescent receive the greatest rainfall. The Fertile Crescent is prone to large variation in rainfall, with changes from winter-dominated to winter/spring-dominated seasonal patterns of rainfall, travelling northeast from the Mediterranean coast into the Taurus-Zagros Mountains and Iranian plateau (Stevens et al., 2001). Winter in the Fertile Crescent is dominated by cold, dry air from the Siberian Anticyclone, but this season (November-April) can be relatively wet due to the penetration of moisture-bearing depressions that transport water vapour from either the Atlantic or the Mediterranean (Stevens et al., 2001). Summers in the Fertile Crescent are hot and dry, and rapid cooling of the land in autumn tends to stabilise the atmosphere, lengthening the dry season (May-October) (Stevens et al., 2001). Conversely, rapid cooling of the land in spring (notably April) is associated with a destabilisation of the atmosphere, creating the opportunity for thunderstorms (Stevens et al., 2001).

The variability and reliability of annual rainfall across the Fertile Crescent area can present serious problems for crop farmers (Riehl, 2012). Drought is a significant issue within this geographic area (Barlow et al., 2016), and is driven primarily by lack of precipitation, but complex associations between precipitation, changes in temperature and other meteorological processes can variously exacerbate or alleviate drought conditions (Sheffield and Wood, 2008). In these arid/semi-arid climates, anomalously high temperatures will increase evapotranspiration and low precipitation will reduce recharge of the soil column, but drought induced by many months of below average rainfall and maintained by high temperatures could be alleviated by a single storm (Sheffield and Wood, 2008). Today, the arid/semi-arid climate experienced in the study region exerts a major strain on freshwater resources and the variability in summer temperatures and precipitation has significant implications for agriculture and human health (Barlow et al., 2016).

2.2.3.2 Current vegetation of southwest Asia

Biomes are large geographic areas that are characterised by the shared traits of the dominant plant species, which reflect their adaptation to particular environmental conditions (Woodward et al., 2004). Prentice et al. (1992) developed a global biome model that characterizes natural plant communities based on plant physiology and dominance, soil properties and climate (precipitation and temperature), and today the Fertile Crescent is chiefly characterized by the warm grass/shrub vegetation biome (Prentice et al., 1992: Figure 1b). The warm grass/shrub vegetation biome is associated with climates where the mean warmest-month temperatures exceed 22°C and where there is sufficient annual precipitation to meet 18-28% of demand, which is adequate for tropical or sub-tropical grasses but not for succulents or thorn bushes (Prentice et al., 1992, p. 131). There are limited areas within the Fertile Crescent (restricted to the southern Levant and southeast Turkey) that are characterized by the xerophytic woods/scrub biome, which is typically composed of pine, juniper and oak scrub (Prentice et al., 1992: Figure 1b). This type of vegetation, dominated by evergreen shrubs and sclerophyllous trees, is particularly adapted to the distinctive Mediterranean climatic regime of summer drought and cool wet winters, with only sporadic episodes of frost (Roberts et al., 2011). The coastal regions of the Fertile Crescent (i.e. parts of the Levantine Corridor and southeast Turkey) experience eastern Mediterranean climate regimes, and the peak vegetative growth under Mediterranean climate conditions is in spring, which coincides with moist soil conditions and rising temperatures, or autumn, after the first rains (Roberts et al., 2011).

Investigation of the current distribution of wild cereal and pulse progenitors within southwest Asia (e.g. Willcox, 2005, Zohary et al., 2012) has been a useful line of enquiry in identifying the potential locations of domestication (e.g. Willcox et al., 2009). Broadly speaking, the founder cereal progenitors *Triticum baeoticum* Boiss. emend. Schiem. (wild einkorn), *T. dicoccoides* (Körn. ex. Aschers. & Graebner) Schweinf. (wild emmer) and *Hordeum spontaneum* C. Koch (barley) occur in the slightly dry, more open parkland steppe, with dispersed shrubs, wild almond trees and oaks (Fuller, 2007, Zohary et al., 2012). The distributions of the wild cereal progenitors are not uniform, however, being variously restricted by climate, soil chemistry and precipitation regimes (Willcox, 2005). Wild *Triticum* (wheat) species are calcifuge and as such favour more acid soils formed on basalt bedrocks or de-calcified alluvial soils, which are not widely distributed in the region (Willcox, 2005). Similarly, wild *Secale* (rye) species, including wild secondary progenitor *Secale vavilovii* Grossh, are also calcifuges that thrive in basaltic bedrocks (Zohary et al., 2012). Wild progenitor *Triticum baeoticum* is widely distributed across southwest Asia, but predominantly occurs in the northern regions of the Fertile Crescent (Zohary et al., 2012) and, along with wild *Secale* (rye), can be found in habitats up to 500 m a.s.l. (Willcox, 2005). There is regional variation in the distribution of *Triticum baeoticum*: in the north and northwest regions of its natural distribution, a one-grained form (known as *T. aegilopoides* (Link) Bal.) is the predominant form and, in the southern areas of its distribution, the two-grained form (*T. thaoudar* Reuter) dominates (Zohary et al., 2012). Intermediate forms of one-grained and two-grained *Triticum baeoticum* are also frequent in areas of central Anatolia/Transcaucasia and parts of Iran (Zohary et al., 2012). Another species of wild wheat, *Triticum urartu* Tuman., which closely resembles the two-grained form of *T. baeoticum* (*T. thaoudar*), favours basaltic soils and frequently forms mixed stands with *T. baeoticum* (Zohary et al., 2012).

Triticum dicoccoides has a more restricted geographic distribution and range of ecological preferences than *T. baeoticum*, and its natural distribution tends to be concentrated in the Upper Jordan Valley, within the Levant (Zohary et al., 2012). In the northern and eastern regions of its distribution, *Triticum dicoccoides* has been found to grow with *T. araraticum* Jakubz. (Zohary et al., 2012)*.* In terms of edaphic preferences, *Triticum dicoccoides* is restricted to soils formed on basaltic and hard limestone bedrocks, and does not grow on marls or chalks (Zohary et al., 2012). Rainfall also forms a north-south environmental gradient for the distributions of different species, especially wheat; in the moister conditions of the north and lower ranges of the Taurus, mixed stands of wild *Triticum dicoccoides* and *T. baeoticum* can be found (Willcox, 2005). *Triticum dicoccoides* is absent from regions that receive less than 400 mm of rain per year, whilst *Triticum urartu* and *T. baeoticum* reach as far north as the Syrian/Turkish border and can grow in more southerly areas where the annual rainfall is 300- 350 mm (Willcox, 2005). Conversely, *Hordeum spontaneum* (the wild progenitor of barley) is

more widespread across much of southwest Asia, but is particularly common in deciduous oak park-forest belt situated to the east, north and west of the Syrian Desert, the Euphrates basin and on the slopes facing the Jordan Rift Valley (Zohary et al., 2012). Being more tolerant of calcareous soils and arid climates (Zohary et al., 2012), *Hordeum spontaneum* can grow in nutrient-poor areas with 200-250 mm of rain per annum, although it seems to be less adapted to colder conditions than *Triticum* and *Secale* species, which may be attributed to its tendency to ripen earlier than other wild cereals (Willcox, 2005). In addition, *Avena sterilis* L. (one of the likely progenitors of secondary domesticate *A. sativa* L.) is also widely distributed across the Fertile Crescent and frequently grows with wild wheats and barley (Zohary et al., 2012). *Avena fatua* L. (a wild species of oat that is also a potential progenitor of *A. sativa*) has a weedy growth habit, rarely occurring in primary (natural) habitats, but grows well in colder, more continental conditions (Zohary et al., 2012).

Within southwest Asia, the wild pulse progenitors tend to occur in the north-eastern region of the Fertile Crescent (including parts of Turkey, Syria, Jordan, Israel, northern Iraq and northern Iran) (Willcox, 2005, Zohary et al., 2012). The two species of wild *Pisum* (pea) that are considered the likely progenitors of *P. sativum* L. (*Pisum elatius* M. Beib. and *P. humile* Boiss. & Nöe) have regional geographic distribution patterns within the Mediterranean basin and southwest Asia (Zohary et al., 2012). *Pisum elatius* occurs throughout the Mediterranean basin and particularly thrives as a sporadic climber in maquis (i.e. predominantly evergreen scrubland) vegetation within the wetter (more mesic) parts of the region. The natural distribution of wild progenitor *Pisum humile* is restricted to southwest Asia, and this species typically grows in deciduous park-forest belts and in open, steppe-like herbaceous vegetation, which are similar habitats to those favoured by the wild wheats and barley (Zohary et al., 2012). The natural distribution of wild progenitor *Lens orientalis* (Boiss.) Shmalh. (lentil) includes the Mediterranean basin, south-western and central Asia (Zohary et al., 2012). Within the study region, *Lens orientalis* is primarily found in the northern arc of the Fertile Crescent, in present-day northern Israel, Syria, southern Turkey, northern Iraq and western Iran (Zohary, 1972a). *Lens orientalis* is typically found growing on gravelly hillslopes and in stony habitats in steppe-like herbaceous vegetation in small, scattered colonies (Zohary, 1972a), and frequently grows alongside wild forms of *Vicia ervilia* (L.) Willd. (Zohary et al., 2012). Wild progenitor *Cicer reticulatum* Ladiz. (chickpea) is particularly restricted in terms of its geographic distribution, only occurring in southeast Turkey and northern Syria, and thrives on limestone bedrock (Abbo et al., 2008b, Zohary et al., 2012).

2.2.4 Palaeoenvironment of southwest Asia

2.2.4.1 Palaeoclimatic events of the Late Pleistocene/early Holocene transition In the following discussion, the environmental chronologies follow Maher et al. (2011). The global shift from glacial conditions during the Late Pleistocene to the interglacial conditions of the Holocene (around 11.7 kyr cal. BP), had a profound effect on the environment worldwide, causing rises in sea level, alterations in atmospheric and oceanic circulation systems (Alley, 2000b, Denton et al., 2005, 2006, Broecker et al., 2010) and shifts in vegetation zones (Moore and Hillman, 1992). Significant data sources for palaeoclimate reconstructions are derived from geochemical, mineral and biological materials (such as those of marine, continental, biologic, volcanic, atmospheric, and extra-terrestrial origins) preserved in incremental deposits of ice from ice-cores, sediment from ocean-cores, palaeosols and peat deposits, and growth bands from cave speleothems. Such evidence provides high-resolution multiproxy indicators of past climates that are inter-relatable, the analysis of which has enabled regional reconstructions for the Fertile Crescent, which can be related to global scale palaeoclimate models (e.g. Bar-Matthews et al., 1997, 2003, Robinson et al., 2006, Pustovoytov et al., 2007, Riehl et al., 2009, Orland et al., 2012, Torfstein et al., 2013). However, palaeoclimate reconstructions that hinge on evidence from single sites or records can be difficult to extrapolate to more generalised models on a regional scale, and there is a danger of oversimplifying the interpretation of such palaeoclimatic records and obscuring inter-regional differences in past climatic regimes (Enzel et al., 2008). Obtaining off-site palaeoclimate data that are local to archaeological sequences can also be difficult. For example, as Willcox (2012a) noted, there are no palaeoclimate records (such as those from lake sediments) in the middle Euphrates region in northern Syria that could be related to the Syrian sites of Jerf el Ahmer, Mureybet and Abu Hureyra.

The Late Glacial Maximum (LGM) is characterised by persistent cold and dry conditions, as evidenced in a study of isotopic temperature records from Greenland ice-cores that are compared with changes in snowlines in the Northern Hemisphere, preserved in the moraine sequences from North Atlantic marine sediment cores (Denton et al., 2005). Palaeoclimate simulations of the LGM have been produced by Willmes et al. (2017) using high-resolution palaeoclimate data relating to temperature and precipitation (obtained from the Coupled Model Intercomparison Project (CMIP) and the Paleo Model Intercomparison Project (PMIP) climate model simulation data (see Braconnot et al., 2011, 2012)), to compute Köppen-Geiger classifications. These simulations indicate that during the LGM the Fertile Crescent was predominantly characterised by cold arid steppe climates (BSk), where the annual mean temperatures are predicted to be below 18°C (Willmes et al., 2017), with cold arid desert

climates (BWk) encroaching on the western side of the Levantine corridor and lower reaches of the Taurus-Zagros Mountain ranges (Figure 2.5). In addition, around the coastal region of the northern Levant (including Syria and southern Turkey), warm and temperate climates, associated with hot, dry summers and cool, wet winters (Csa) are predicted during this period (Figure 2.5). Analyses of air trapped in ancient polar ice from Antarctic ice-cores have also enabled reconstructions for the levels of $CO₂$ in the atmosphere over the past 220, 000 years (e.g. Barnola et al., 1987, Neftel et al., 1988, Jouzel et al., 1993, Monnin et al., 2001, Lemieux-Dudon et al., 2010). The levels of atmospheric $CO₂$ during the Late Pleistocene have been identified as a constraining factor in the process of plant domestication (as outlined in Section 1.3), and during the LGM atmospheric $CO₂$ was low (~18 Pa), but began to increase around 17 kyr cal. BP (Figure 2.6).

A decline in oxygen-isotope ($\delta^{18}O$) values preserved in ancient polar ice from Greenland shows that a rapid cooling event occurred around 16.8-16.5 kyr cal. BP, known as the Heinrich 1 event (Bond and Lotti, 1995, Denton et al., 2005). Heinrich events are associated with abrupt influxes of large volumes of freshwater into the Atlantic Ocean derived from icebergs dumped from glaciers in the northern hemisphere (Heinrich, 1988, Bond and Lotti, 1995, Bassis et al., 2017). Corresponding oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotope signals for the Heinrich 1 event have also been observed in terrestrial cave speleothem records from the Levant (in Israel and Lebanon), where sudden increases in δ^{18} O and δ^{13} C indicate a decline in temperature and precipitation at 16.5 kyr cal. BP (Bar-Matthews et al., 1999, 2003). The lowering of lake levels detected in Lake Lisan sediment sequences (the late glacial counterpart of the Dead Sea in the Jordan Rift Valley) and reduced δ^{18} O of planktonic foraminifera preserved in eastern Mediterranean marine sediments also indicate regional climatic cooling that coincides with the Heinrich 1 event (Bar-Matthews et al., 1999, 2003, Bartov et al., 2003, Torfstein et al., 2013, Cheng et al., 2015). Heinrich events seem to immediately precede abrupt shifts to warmer climates that are almost as high as interglacial temperatures (Bond et al., 1993, Bond and Lotti, 1995), and Heinrich 1 coincides with the onset of the warm and wet Bølling-Allerød interstadial (14.6-12.9 kyr cal. BP) (Maher et al., 2011). The Bølling-Allerød interstadial was marked by a stalling of the rising trend in atmospheric $CO₂$ (approaching ~24 Pa) that characterised the end of the glacial period (Figure 2.6).

The Bølling-Allerød interstadial is well documented in global palaeoclimate records from the Northern Hemisphere (e.g. Alley, 2000a, Monnin et al., 2001, Weaver et al., 2003, Shakun and Carlson, 2010) and was a prolonged phase of climatic amelioration (Maher et al., 2011). The melting of Antarctic ice sheets triggered the Bølling-Allerød interstadial, in an event called Meltwater Pulse IA, which released freshwater causing rises in sea level and disrupted ocean

circulation systems (Weaver et al., 2003). Within southwest Asia, palaeoclimate records provide corroborative evidence that the Bølling-Allerød interstadial was a warm and wet interval during the glacial termination in this region. For instance, decreases in $\delta^{18}O$ levels in the Soreq cave speleothem records indicate increases in temperatures and moisture (precipitation) during this interstadial (Bar-Matthews et al., 1999). Likewise, the development of red Mediterranean Soil (terra rossa soils) and increased sedimentation recorded in palaeosols from sites in the southern Levant, together with detected rises in the levels of Lake Lisan observed in lacustrine sediment sequences, indicate increased precipitation during this period (Goldberg and Schuldenrein, 1981, Cordova, 2000, Gvirtzman and Wieder, 2001, Bartov et al., 2002, 2003, Torfstein et al., 2013). Towards the end of the Bølling-Allerød interstadial, an increase in δ^{18} O concentrations preserved in Greenland ice-core palaeoclimate records shows evidence for a gradual cooling that was punctuated by a century-long cold plunge before the onset of the Younger Dryas (Broecker et al., 2010, p. 1079).

The Younger Dryas, a millennial-duration cold snap (12.9-11.7 kyr cal. BP), immediately preceded the Holocene (Broecker et al., 2010). The Younger Dryas was a significant arid phase in the Northern Hemisphere (Alley, 2000b, Broecker et al., 2010, Shakun and Carlson, 2010) and is detectable in palaeoclimate records from the eastern Mediterranean and southwest Asia (e.g. Bar-Matthews et al., 1997, 1999, Gvirtzman and Wieder, 2001, Stevens et al., 2001, Wick et al., 2003, Leroy et al., 2013, Sharifi et al., 2015). Global palaeoclimate reconstructions indicate that during the Younger Dryas, processes affecting North Atlantic oceanic heat transport (attributed to increased precipitation or influxes of meltwater from the Arctic), resulted in the cooling of the North Atlantic (Alley, 2000b, Denton et al., 2005). This North Atlantic cooling in turn led to a reduction in the strength of the African and Asian monsoons (resulting in drier conditions) and steeper temperature gradients causing stronger winds (Alley, 2000b, pp. 222-223, Brauer et al., 2008). This interpretation of ice and ocean-core records (Alley, 2000b, Denton et al., 2005, 2006, Brauer et al., 2008) is supported by other palaeoclimate data that indicate that the Younger Dryas was extremely arid and dusty (Stevens et al., 2001, Robinson et al., 2006, Sharifi et al., 2015) and so cold as to approach conditions of the full glacial (Moore and Hillman, 1992). A sharp increase in δ^{18} O values from speleothems in Soreq Cave, Israel, and accumulations of loess material in palaeosols from sites in Israel and Iran, document intensively dry, dusty and cool conditions during the Younger Dryas within the region of the Fertile Crescent (Bar-Matthews et al., 1999, Gvirtzman and Wieder, 2001, Sharifi et al., 2015). Regional palaeoclimate records show overall decreased precipitation, decreased seasonality, and lowered lake levels in the eastern Mediterranean and parts of southwest Asia (e.g. Gvirtzman and Wieder, 2001, Bartov et al., 2002, 2003, Wick et al., 2003, Orland et al.,

2012, Cheng et al., 2015). During this interval, analysis of concentrations of CO₂ trapped in bubbles within Antarctic ice-core records also show that there was a rapid increase in CO₂ from ~24 Pa to ~26 Pa (Figure 2.6).

The end of the Younger Dryas (11.7 kyr cal. BP) marks the end of the Pleistocene and the termination of the last glacial. A sharp drop in $\delta^{18}O$ concentrations preserved in Greenland ice cores show that the transition from the cold and arid conditions of the Younger Dryas to the warm interglacial conditions of the Pre-Boreal Holocene (11.7 to 10.7 kyr cal. BP) was abrupt, being merely a matter of tens of years or potentially less (Alley et al., 1993, Alley, 2000b, Broecker et al., 2010). Regional evidence for decreases in δ^{18} O, however, derived from terrestrial cave speleothems in the Levant (Jeita Cave, Lebanon, and Soreq Cave, Israel) indicate that the transition from the Younger Dryas to the early Holocene took at least 500 years (Verheyden et al., 2008). The apparent discord between the Greenland ice-core and Levantine cave speleothem palaeoclimate records may reflect global climatic processes that manifested in the North Atlantic region, being more gradual further away from the Atlantic (Verheyden et al., 2008, see also Shakun and Carlson, 2010). The termination of the Younger Dryas is also associated with a global expansion of wetlands, as inferred by an increase in the concentration of methane trapped in air bubbles in ice-core records from central Greenland (Alley, 2000b). The development of terra rossa soils and increased rates of sedimentation observed in soil sequences from sites in the southern Levant also attest to the wetter conditions of the early Holocene compared to the Younger Dryas (Goldberg and Schuldenrein, 1981, Cordova, 2000, Gvirtzman and Wieder, 2001). Furthermore, decreases in windblown lithogenic materials and compound-specific leaf wax hydrogen isotope (δD) levels recorded in peat cores from Neor Lake, north-west Iran, provide supporting evidence that the early Holocene was a relatively wet period with low aeolian input, compared to the dry and dusty conditions of the Younger Dryas (Sharifi et al., 2015). Decreases in δ^{18} O documented in speleothem isotope records from the southern Levant (Soreq Cave and Peqiin Cave in central and northern Israel respectively), in conjunction with low δ^{18} O values recorded in planktonic foraminifera isotopic records from the eastern Mediterranean (see Bar-Matthews et al., 2003), indicate that the early Holocene was probably the wettest phase of the last 25,000 years for much of this area (Bar-Matthews et al., 1997, 1999, 2003, Robinson et al., 2006). Overall, the Late Pleistocene was a period that experienced episodic fluctuations in precipitation (Colledge and Conolly, 2010), with the isotopic records preserved in speleothems from sites in the Levant indicating little seasonal variation, whilst the early Holocene was extremely wet with more pronounced seasonal precipitation (Robinson et al., 2006, Orland et al., 2012).

Whilst signatures for significant climatic events that occurred in the Northern Hemisphere (such as the Bølling-Allerød interstadial and Younger Dryas) are preserved in climatic records from sites within the Fertile Crescent, there may be evidence for regional variation in the hydroclimate records. For example, Cheng et al. (2015) observed evidence for relatively wetter conditions in the northern Levant compared to the southern Levant during the last glacial terminal, as inferred from the isotopic composition of Jeita Cave speleothems compared with Soreq and Peqiin Caves and Dead Sea level records. The Dead Sea basin is situated in the Jordan Rift Valley (that includes parts of present-day Israel, Jordan and Palestine), and Dead Sea levels are a significant consideration in regional palaeoclimate reconstructions, as they reflect hydrological conditions over its large watershed in southern Levant (Bartov et al., 2002, Torfstein et al., 2013, Cheng et al., 2015, p. 8647). In the southern Levant, decreased precipitation during the Heinrich 1 event led to a significant fall in the Dead Sea level (around 16 kyr cal. BP) (Bartov et al., 2003), which coincides with wetter conditions in the northern Levant, as indicated by increases in $\delta^{18}O$ and $\delta^{13}C$ in the Jeita Cave speleothem records (Cheng et al., 2015: Figure 3). They propose that such regional variation in hydroclimates may be attributed to the effects of boundaries in atmospheric circulation systems between the northern and southern Levant (Cheng et al., 2015). During the early Holocene, however, there is evidence of a recovery of the Dead Sea, with increased lake levels just after 10 kyr cal. BP (Cheng et al., 2015: Figure 3). This recovery of the Dead Sea supports evidence for increased precipitation during the early Holocene, as the precipitation component of the regional hydrological cycle is the greatest causal factor of the lake level fluctuations (Torfstein et al., 2013).

In sum, the global climatic changes associated with the transition from glacial to interglacial conditions during the Late Pleistocene and early Holocene, as documented in ice- and marinecore climate records, are also apparent in marine and terrestrial climate archives from the eastern Mediterranean region and sites within the Fertile Crescent (e.g. Bar-Matthews et al., 1997, 1999, 2003, Verheyden et al., 2008). Within the Northern Hemisphere, the effects of large-scale climatic shifts during the last glacial terminal (including the Heinrich 1 event, the Bølling-Allerød interstadial, the Younger Dryas, and onset of the early Holocene) were experienced in vast areas of continental northwest Europe and Asia. However, multi-proxy climate indicators from sites in the Fertile Crescent and eastern Mediterranean region indicate that there is climatic variation on a sub-continental scale during the Late Pleistocene/early Holocene transition. The global climatic events that mark the end of the last glacial period and beginning of the current interglacial, potentially manifested more gradually and with less

amplitude in southwest Asia than in the North Atlantic region, due to complex interactions with atmospheric and marine circulation systems during these periods.

2.2.4.2 Implications of the palaeoclimate for southwest Asian vegetation

While palaeoclimate records indicate that the amplitude of climate variability was reduced during the Holocene relative to the preceding glacial period (e.g. Grootes et al., 1993), caution has been voiced about the supposed climatic amelioration experienced following the end of the Pleistocene. Whilst overall the early Holocene experienced increased moisture, Stevens et al. (2001) draw attention to the fact that the seasonal distribution of this moisture would have differed to that of today, whereby spring rains were rare or completely absent, which would prolong the period of summer drought in the eastern region of the Fertile Crescent. In Stevens et al.'s (2001) study, the $\delta^{18}O$ isotope records from lacustrine carbonate deposits from Lake Zeribar, western Iran, are compared with five hypothetical climate regimes using modern $\delta^{18}O$ values for precipitation at Senyurt and Dalbahce, Turkey (which are considered to best represent the geographic conditions of the catchment of Lake Zeribar), in order to identify early Holocene precipitation patterns. Based on these climate regime models, decreased and low δ^{18} O values during the early Holocene indicate that spring/summer rains were infrequent and that winter snows were the main source of moisture for the eastern region of the Fertile Crescent (Roberts et al., 2001). Furthermore, changes in the weather systems have been identified as causal links to high rainfall along the Mediterranean coast during the early Holocene (notably enhancement of the African monsoon or more frequent winter depressions) and wetter conditions in central Turkey, due to storm tracks, but these impacts did not reach further inland (Stevens et al., 2001). In addition, climate changes that may have affected water transport and subsequent precipitation associated with southerly fluxes (such as the Indian Monsoon) could have had a disproportionally strong effect on the total precipitation in eastern areas of the Fertile Crescent, despite the main source of water for precipitation being to the west (Evans and Smith, 2006). The view that the early Holocene was characterised by a dominant arid phase attributed to the precipitation regimes (i.e. long summer droughts), is supported by peaks of *Chenopodium rubrum* seeds from lacustrine deposits from Lake Zeribar (Wasylikowa, 2005), the prevalence of *Pistacia* and the scarcity of *Quercus* (the latter is a less drought-tolerant species) that are variously recorded in a number of palynological studies from sites in Iran, Turkey and the Caspian Sea (Wasylikowa et al., 2006, Djamali et al., 2010, Kaplan, 2013, Leroy et al., 2013, Aubert et al., 2017).

The first two millennia of the Holocene (encompassing the Pre-Boreal and early Boreal periods) were, therefore, an era of significant short-to-medium-term ecological instability that was particularly pronounced in the climatically sensitive, semi-arid continental interiors of

southwest Asia (Asouti, 2017). The climatic oscillations that took place during the Late Pleistocene/early Holocene transition had a major impact on vegetation biomes across the Fertile Crescent. Integrated pollen records and multi-proxy palaeoclimate data from marine and terrestrial locales throughout the Mediterranean and southwest Asia provide the basis for vegetation reconstructions during the Late Pleistocene/early Holocene transition (e.g. Rossignol-Strick, 1995, Roberts et al., 2001, Woldring and Bottema, 2001/2002, Wick et al., 2003, van Zeist, 2008, Deckers et al., 2009, Litt et al., 2009). In broad terms, the ecotonal areas between the Mediterranean temperate woodlands (in the region of the southern Levant) and the Irano-Taurean steppe cycled between dominance of forest under warmer/moist climates (notably the Bølling-Allerød interval and the Pre-Boreal) and a predominance of steppic (drought tolerant) species under drier conditions (in this case the Younger Dryas) (Robinson et al., 2006, Rosen and Rivera-Collazo, 2012). These episodes of ecological instability would have had significant implications in terms of the changing character of the landscape, and the distribution and predictability of available resources (Bar-Yosef, 2011, Rosen and Rivera-Collazo, 2012, Asouti, 2017).

There is broad consensus in the regional pollen records that there was a shift from Chenopodiaceae and other dry, cool steppic species to more forested conditions at the end of the Late Glacial Maximum, with a brief return of these arid-adapted plants associated with the Younger Dryas (Rossignol-Strick, 1995, Deckers et al., 2009). The distribution of vegetation during the relatively warm and wet Bølling-Allerød interstadial reflected the bioclimatic zones of the Fertile Crescent; grassland vegetation (including *Cerealia*) dominated the inner Anatolian landscape, and was associated with a sparse, low-density tree cover (principally members of the Rosaceae family and *Pistacia*, with low representation of *Juniperus* and deciduous *Quercus*) (Roberts et al., 2001, Woldring and Bottema, 2001/2002, Litt et al., 2009, Asouti and Kabukcu, 2014, Kabukcu, 2017). In comparison, the western Levantine littoral (coastal) areas were dominated by trees, and in the Zagros Mountain range, sparsely wooded *Pistacia* grasslands prevailed (van Zeist, 2008). As the climate changed during the Younger Dryas, there is evidence for the expansion of grasslands at the expense of oak woodlands in the Levantine littoral, and this has been interpreted as indicating the better adaptation of grasses to compete for finite groundwater resources, compared to trees under the cold and arid conditions of this climatic period (Asouti and Kabukcu, 2014, p. 168, Asouti, 2017). A concurrent decline in oak and the coeval expansion of *Artemisia*-Chenopodiaceae steppe, rather than grassland, is observed further north in the Syrian Ghab Valley catchment (Wright and Thorpe, 2003). An expansion of *Artemisia*-Chenopodiaceae steppe is also seen in the more continental inland regions of central and eastern Anatolia, but here this coincides with a

retreat in grassland (Roberts et al., 2001, Woldring and Bottema, 2001/2002, Wick et al., 2003). In the Zagros Mountain ranges, *Artemisia-*Poaceae steppe replaces the *Pistacia* grasslands during the Younger Dryas (van Zeist, 2008).

The first two millennia of the Holocene saw a dramatic expansion of grasslands (including cereal progenitor taxa), which reached their greatest extent during this period in southwest Asia (Rossignol-Strick, 1995, Roberts, 2002, Asouti, 2017), and a rise in *Pistacia* (Rossignol-Strick, 1995, Roberts et al., 2001, Wick et al., 2003). During this period, peaks in wildfire signals have been observed in micro-charcoal records from lacustrine sediment sequences from Lake Akgöl, central Turkey, Lake Hula, Israel, Lake Eski Acrgöl, central Anatolia, Ghab, north-western Syria and Lake Van, south-eastern Turkey (see Turner et al., 2010). These peaks in wildfire signals have been linked to the climate of the early Holocene, wherein increased seasonality of precipitation, characterised by higher winter rainfall during this period, in combination with hot, dry summers, resulted in an increase in biomass production throughout southwest Asia, with seasonal drying out of plant biomass (Turner et al., 2010). Thus, swathes of grassland were susceptible to wild fires during the hot and dry summer months that characterise the early Holocene for much of the region (Turner et al., 2010). Furthermore, the charcoal and pollen records from regional lacustrine sediments indicate that wild fires during this period may have contributed to the delay in deciduous oak expansion (Wick et al., 2003, Turner et al., 2010), which is associated with the first three millennia of the Holocene (Roberts et al., 2001). Regional pollen records indicate that only from the mid-late Holocene did trees become a significant component of the vegetation of continental inland southwest Asia (Bottema, 1986, Wick et al., 2003, Djamali et al., 2008, van Zeist, 2008, Litt et al., 2009). As well as climatic impacts on vegetation, Roberts (2002, p. 1008) also ventures that the frequent fire disturbances experienced during the early Holocene may have been partly natural and partly human-induced, the latter as a result of potential environment engineering (such as systematic burning to control and regulate vegetation), in order to encourage more open habitats that are favourable for grazing or cultivation. Overall, the early Holocene climatic amelioration is believed to have prompted the emergence of highly productive and stable resource environments (Savard et al., 2006, Asouti, 2017), and it has been suggested that this may have been an important factor for encouraging sedentism in favourable ecotones, which offered a diverse range of resources both locally and seasonally (Savard et al., 2006). Within these resource-rich environments of the Pre-Boreal Holocene, however, it has been argued that there was still 'meso-microecological instability', which may have led hunter-gatherer groups to develop local distinctive 'resilience' strategies (Asouti, 2017, p. 24).

2.3 Archaeological background

2.3.1 Overview

In this section, the cultural and demographic context of the transitional period from the semisedentary hunter-gatherer societies of the Late Pleistocene to the food producing communities of the early Holocene are discussed. Throughout the Late Pleistocene and early Holocene there were a number of regionally restricted cultural entities that variously interacted or existed independently of one another (Byrd, 2005). Equally varied was the rate and nature of the changes in social organisation and economic strategies of the cultural groups, with regional distinctions between the southern Levant (including Israel, Palestine, Jordan and Lebanon), the northern Levant (Syria and south-eastern Turkey), and the eastern region of the Fertile Crescent (i.e. the upper Tigris basin and Taurus-Zagros Mountain range) (Byrd, 2005, Goring-Morris et al., 2009). The cultural chronologies used here follow Goring-Morris et al. (2009) and the regional classification of Late Epipalaeolithic and Early Neolithic site locations (i.e. those located in the southern Levant, the northern Levant or the eastern Fertile Crescent) follow Wallace et al.'s (2019: Figure 7) classification for the geographic regions of the Fertile Crescent.

The advent of early plant management strategies occurred during the Late Pleistocene (c. 14.6- 11.7 kyr cal. BP) and is associated with Late Epipalaeolithic hunter-gatherer societies. The termination of the last glacial period (the Pleistocene) and the onset of the Holocene is associated with the Pre-Pottery Neolithic (PPN) period, the early phase of which (PPNA – 11.7- 10.7 kyr cal. BP) saw the development of a range of pre-agricultural plant and animal management practices that have been collectively categorised as 'low-level food production' (Smith, 2001, Asouti and Fuller, 2013, Zeder, 2015, Asouti, 2017). The emergence of agriculture as the primary subsistence base, wherein economies became principally dependent on domesticated plants (Zeder, 2015, pp. 2-3), did not occur until the later PPNB (~10.7-9 kyr cal. BP) (Weiss et al., 2006, Zohary et al., 2012).

2.3.2 Cultural context

2.3.2.1 Late Pleistocene

As discussed by Savard et al. (2006, pp. 192-193), there is a lack of consensus on how to label pre-agrarian settlement sites in southwest Asia, because the sites are not easily classified within strict chrono-cultural categories. Late Epipalaeolithic settlement sites in the southern and northern Levant are typically associated with the Natufian cultural groups, whilst those in the northern and eastern regions of the Fertile Crescent have been described by some as

'Round House Horizon' cultural entities (see Rosenberg et al., 1998, Peasnall, 2000, Savard et al., 2006, p. 183). Archaeological evidence for occupation activity in the northern and eastern parts of the Fertile Crescent is sparse prior to 13.3 kyr cal. B.P in comparison with the Levantine Corridor (Figure 2.7), and it remains uncertain whether this reflects the low intensity of settlement activity or gaps in available evidence for this region (Byrd, 2005). Furthermore, the Round House Horizon cultural groups identified in the Late Epipalaeolithic (Round House, phase 1) appear to persist into the early Holocene (Round House, phase 2), unlike the Late Natufian cultural groups of the Levantine Corridor (Rosenberg et al., 1998).

Broadly speaking, the cultural periods during this socially and economically transitional phase coincide with significant climatic events that mark the termination of the Late Glacial Maximum and the onset of the Holocene. The Early Natufian societies of the Late Epipalaeolithic flourished during the favourable climatic conditions associated with the Bølling-Allerød interstadial (14.6-12.9 kyr cal. BP), the Late Natufian and Round House (phase 1) societies were present during the cold and arid Younger Dryas (12.9-11.7 cal. BP) (Table 2.1). The cultural periods associated with the Late Epipalaeolithic tend to pre-date these climatic events, and so are unlikely to be associated with climate change (Maher et al., 2011). Furthermore, responses to changes in climate would not necessarily have been uniform across the region during this time. The perception of climatic deterioration can also depend on the individual circumstances of particular groups. For example, if a hunter-gatherer group has not invested in a particular location or food resource (such as suitable land for cultivating specific plants), vegetation response to changes in climatic conditions may have little impact on food procurement strategies (Roberts et al., 2018).

The Late Epipalaeolithic hunter-gatherer groups practised subsistence-based economies, characterised by 'food procurement' activities (collecting wild plant resources) in the Early Natufian period and progressed to 'low-level food production' practices (including plant management and the cultivation of non-domesticated species) in the Late Natufian period (Smith, 2001, Byrd, 2005). Zooarchaeological evidence recovered from Late Epipalaeolithic sites shows that the subsistence strategies also included specialised hunting of medium-sized animals, especially gazelle, and over time the exploitation of avifauna, supplemented by fishing, where possible (Tchernov, 1993, Munro et al., 2004, Goring-Morris et al., 2009). Settlement patterns indicate that sedentism initially began in the resource-rich centre of the Mediterranean woodland, associated with Early Natufian groups, and involved the aggregation of multiple social groups for at least nine months of the year, with a heavy focus on the exploitation of plant resources (including annual grasses, legumes and nuts) (Byrd, 2005). Bioarchaeological indicators for sedentism in the Late Epipalaeolithic include an increase in the

appearance of human commensal species, such as mice, rats and sparrows (Tchernov, 1991), compared to forager sites, as well as evidence for hunting during the summer and winter months based on the analysis of cementum increments on gazelle teeth (Bar-Yosef, 1998, Bar-Yosef, 2001). The stone tool assemblages of this period (including heavy, undressed stones), burial practices (the digging of graves), evidence for permanent storage facilities, and investment in the construction of settlement sites also indicate long-term occupation (Bar-Yosef, 1998, 2001). Some of the sedentary Natufian sites occupied 'junctions' between different environmental zones, potentially maximising the range of resources available for exploitation (Henry, 1989 pp.182-185, 1997 p.109), while others were located in prominent parts of the landscape, such as caves and rock shelters, the latter of which may have been desirable for defensibility and/or storage, particularly of perishable goods (Byrd, 2005). The size and layout of the architectural features of Late Epipalaeolithic settlements, as well as the labour and investment in the production of heavy ground-stone tools (notably heavy-duty mortars that may be used by a number of households), suggest that, during this period, residence patterns were based on units larger than nuclear families (Goring-Morris and Belfer-Cohen, 2003, Belfer-Cohen and Hovers, 2005, Goring-Morris et al., 2009).

The Late Epipalaeolithic also witnessed a shift in food procurement and processing strategies that potentially reflect the growing importance of foods that require more investment of time and energy to collect, process and store, as indicated by changes in tool technology, such as the development of sickles, and the increase in ground stone tools including mortars and pestles (Wright, 1994, Belfer-Cohen and Hovers, 2005, Byrd, 2005). Mortars and pestles have been interpreted as 'communal tools' and are particularly associated with Early Natufian societies (Wright, 1994, Belfer-Cohen and Hovers, 2005). The dominance of pounding tools has been linked to the adoption of sedentary lifeways during the Late Epipalaeolithic, wherein population pressures led to resource-demand imbalances, and necessity to exploit 'lowerranked' locally available resources, such as grasses (Wright, 1994, p. 254). Increasing social complexity and ritualised activity is also evidenced by the appearance of burials in organised cemeteries within and around these sedentary sites (Byrd, 2005), and may have been a powerful and conspicuous means of indicating ancestral ties to the land (Bloch, 1971, Kuznar, 2003, Byrd, 2005). Evidence for storage facilities is scarce at Early Natufian sites, and food may have been stored in baskets (Hastorf and Foxhall, 2017 p.28), which presents problems when attempting to identify and define the use of plants in the archaeobotanical record (Wallace et al., 2019). These sedentary communities also created a new ecological niche, resulting from the accumulation of domestic debris that attracted commensal species (such as mice, rats and

sparrows) (Byrd, 2005, see also Tchernov, 1991), and which would have provided a fertile and disturbed environment that favoured plants that thrive in such habitats.

The Late Natufian settlements were markedly smaller than those in the preceding period and there seems to have been an increase in mobility at this time (Goring-Morris and Belfer-Cohen, 2003, Goring-Morris et al., 2009). In the Taurus-Zagros foothills and the upper reaches of the Tigris and its tributaries, small villages also developed, ascribed to the Round House Horizon (Phase 1) (Goring-Morris et al., 2009), such as the sedentary hunter-gatherer site Hallan Ҫemi, situated in the foothills of the Taurus Mountain range, eastern Anatolia (Rosenberg et al., 1998). This period also coincides with the cold and arid Younger Dryas, which may have impacted on settlement patterns because vegetation, and therefore the availability of plant and animal resources, changed. Within the interior regions of southwest Asia, the archaeological evidence indicates that hunter-gatherer groups may have adjusted their mobility and subsistence strategies to accommodate the climatic impact on resource availability (Goring-Morris et al., 2009, p. 207, Asouti, 2017). The response of these Late Epipalaeolithic groups was to manage catchments that were characterised by diverse ecologies, both geographically and seasonally, encompassing alluvial plains and arboreal habitats (Savard et al., 2006, Asouti and Fuller, 2011, Willcox, 2012b, Riehl, 2012, Henry, 2013). There also appears to have been an expansion of Natufian-related groups northwards, extending up to Abu Hureyra and Mureybet in the Upper Euphrates plains, Syria (Cauvin, 1991, Moore et al., 2000, Bar-Yosef, 2009, Goring-Morris et al., 2009). A shift in the prevalence of stone tools suitable for grinding rather than pounding is also associated with the Late Natufian period (Wright, 1994, pp. 254-55), which may reflect a change in food processing (i.e. an increase in grain processing, rather than nuts) (Dubreuil, 2004, Bar-Yosef, 2009, p. 131, Goring-Morris et al., 2009). A shift from 'heavy-duty' mortars to grinding stones during the Late Natufian may also reflect a shift in social structure, with decrease in use of large 'communallyowned' stone tools to smaller (easier to produce) grinding stones that are used by smaller family units (Belfer-Cohen and Hovers, 2005, p. 304). The Late Natufian period also witnessed increases in symbolic items (both mobile and fixed), together with the expansion and intensification of exchange networks (Goring-Morris et al., 2009). Some scholars have identified these networks as potentially important as part of a food risk-reduction strategy or a means for obtaining non-local but desired food items, such as grain for brewing beer or making bread as part of feasting and other socially cohesive activities (e.g. Hayden et al., 2013, pp. 140, 142).

2.3.2.2 Early Holocene

The late glacial period ended abruptly with the termination of the Younger Dryas, and the start of the early Holocene brought dramatic climatic improvement (Table 2.1). Around this time new cultural groups emerged, collectively identified as PPNA groups, that were distinct from the previous Late Epipalaeolithic socio-economic systems of the Late Pleistocene in terms of settlement size and distribution, and cultural practices (Byrd, 2005, Kuijt and Finlayson, 2009, p. 10969). The PPNA (including Round House, phase 2) is characterised by resource intensification, and attendant increasing sedentism, symbolic behaviours and social complexity, together with the emergence of regionally distinctive corporate institutions and identities (Byrd, 2005, Goring-Morris et al., 2009, Asouti, 2017). Here 'corporate' refers to different individuals and groups who sustain the pooling of resources, both tangible and intangible (such as material spaces, skills and beliefs), in order to secure and maintain their way of life (Gebel, 2010, p. 41).

Nevertheless, the transition between the Late Epipalaeolithic and PPNA cultural periods does appear to have elements of cultural continuity, based on evidence for similar mortuary practices (e.g. Kuijt, 1996) and the continued increase in the occurrence of grinding tools at the expense of pounding tools (e.g. Belfer-Cohen and Hovers, 2005). Figure 2.7 illustrates the distribution of PPNA sites, where archaeobotanical remains have been found, across southwest Asia compared to those of the Epipalaeolithic period (following Wallace et al., 2019). There are more PPNA settlements, widely distributed across the southern and northern Levant than those of the Epipalaeolithic, and there continues to be relatively limited evidence for settlement in the eastern part of the Fertile Crescent (corresponding to Round House, phase 2) during the early Holocene. This period also sees the emergence of three distinct geographic foci of cultural development: 1) the Levantine corridor, 2) the middle Euphrates and 3) the upper Tigris basin (Goring-Morris et al., 2009), which correspond with the three geographic regions of the Fertile Crescent as classified in Figure 2.7 (the southern Levant, the northern Levant and the eastern Fertile Crescent respectively) following Wallace et al. (2019). The PPNA cultural groups constitute "archaic" village societies and, across all three geographic regions, there is evidence for systematic cultivation, supplemented by continued foraging and hunting (Goring-Morris et al., 2009).

PPNA settlements are characterised by aggregated groups, potentially larger than those of the Late Epipalaeolithic, with evidence for increasing symbolic and ritual behaviours associated with corporate social activity (Watkins, 2004, Asouti, 2017). The increasing symbolic behaviours of these PPNA groups are expressed in the form of animal, human and humanoid reliefs and sculptures; pillars, bucrania and other animal bone installations; and engraved

stones, as well as the frequent association of burials with communal structures (Kuijt and Goring-Morris, 2002, Asouti, 2017). Sizable communal structures have been unearthed at a number of sites in the southern and northern regions of the Fertile Crescent, the construction of which would have necessitated significant communal efforts and resources (Kuijt and Goring-Morris, 2002, Goring-Morris and Belfer-Cohen, 2016). Goring-Morris and Belfer-Cohen (2016) highlight a number of these large communal structures which are located in the southern Levant, notably the tower and wall of Jericho (Kenyon, 1983); a massive semisubterranean structure at Wadi Faynan 16 (Finlayson et al., 2011); structures identified as granaries at Jericho and Dhra' (Kuijt and Finlayson, 2009); and a dedicated cemetery in a semicircular or circular (possibly open) area at Wadi Hemmeh (Makarewicz and Rose, 2011). The PPNA sites in the northern Levant are located along the Middle Euphrates at ca. 25 km intervals (Goring-Morris and Belfer-Cohen, 2016, p. 118), where numerous kiva-type subterranean communal structures have been unearthed, the most notable of which include those at Göbekli Tepe (Schmidt, 2010), Jerf el Ahmar (Stordeur et al., 2000) Mureybet (Stordeur and Ibáñez, 2008) and Tell 'Abr (Yartah, 2005). Dedicated food processing areas such as the 'kitchen' at the PPNA site of Jerf el Ahmar, Syria (Willcox, 2002) have also been identified, demonstrating "material investment in food preparation" (Willcox et al., 2009, p. 156) as well as food storage. In the eastern region of the Fertile Crescent (encompassing the Upper Tigris and Zagros Mountains), the distribution of PPNA settlements is sporadic (Figure 2.7), but of note are the communal structures at Gusir Höyük (Karul, 2011) and Hasankeyf Höyük (Miyake et al., 2012), both of which are located along the Upper Tigris. These PPNA sites, with their associated sizable communal structures, may represent foci for activities with symbolic or ritualistic connotations, such as communal food storage, shared or conspicuous consumption (feasting) and mortuary rites (Kuijt and Finlayson, 2009, Goring-Morris and Belfer-Cohen, 2016, Asouti, 2017).

PPNA groups favoured settlement locations with a high water table, such as those near the margins of the steppe, near marshes, along lake margins, on alluvial fans, and beside river banks (Sherratt, 1980, Kuijt and Goring-Morris, 2002, Byrd, 2005). These locations alleviate the reliance on rainfall to sustain plant growth, mitigating against crop failure, and so constitute large areas of land that can be used for cultivation (Bar-Yosef and Meadow, 1995, Bar-Yosef, 2001, Cauvin, 2000, Kuijt and Goring-Morris, 2002). These locations, however, would still have been subject to seasonal and annual variability in the degree of flooding and silt deposition (Bogaard, 2005, p. 184), which would have affected the groundwater levels that would in turn have impacted on short-term food procurement activities and harvest yield. Tool technology during the PPNA indicates that there were further changes in how food was processed, with

even greater emphasis on grinding stones and slabs, rather than the pounding tools of Late Epipalaeolithic hunter-gatherer groups (Wright, 1994, Belfer-Cohen and Hovers, 2005, Byrd, 2005). The first wood working tools appear in the PPNA, including bifacial tools (such as axes) and chisels, which were small and light tools and thought to have been used for clearing brush, chopping and splitting small logs and tree branches, and to construct more permanent structures during this period (Yerkes et al., 2012).

The faunal and archaeobotanical evidence from the PPNB points to the emergence of smallscale herding and intensive crop cultivation through the course of this period (Bogaard, 2005). With regard to social structure, there is emphasis on households as the autonomous units of PPNB societies (Byrd, 2005, Bogaard, 2005), rather than the larger social groups of the preceding PPNA and Late Epipalaeolithic. The emphasis on grinding stones and slabs continues into the PPNB, reflecting continued intensification of food processing (Wright, 1994, Belfer-Cohen and Hovers, 2005). There is also a change in tool technology during the PPNB, to heavier-duty axes that could be used to fell trees and split large logs, that indicates increasing engineering of local landscapes through systematic forest clearance by felling or burning (Yerkes et al., 2012). The felling of large trees also supplied building materials and fuel for the larger structures and settlements developed during the PPNB (Yerkes et al., 2012). Accompanying this, there was an expansion of trading networks, over greater distances, that introduced new goods, such as cowrie shells, natural tar, and obsidian (Kuijt and Goring-Morris, 2002, Goring-Morris and Belfer-Cohen, 2016), and links have been drawn between the emergence of cereal domestication and these strengthening cultural networks (Hayden, 2009).

2.3.3 Plant exploitation, cultivation and domestication

There is a prevailing view that Late Epipalaeolithic hunter-gatherers exploited a broad spectrum of food plants (Weiss et al., 2004a, 2004b, Savard et al., 2006, Willcox et al., 2008, Colledge and Conolly, 2010, Weide et al., 2018). To some extent, this is due to the very rich assemblage of plant remains found at the Upper Palaeolithic cave site of Ohalo II, Israel, where a broad range of wild grasses and other plant species is represented, some 13,000 years prior to plant domestication (Weiss et al., 2004a). Based on the large numbers of fully mature grains at Ohalo II, and ethnographic parallels, these authors identified numerous taxa as likely gathered for consumption, including the grasses (both large- and small-seeded taxa), *Alopecurus utriculatus/arundinaceus*, *Bromus pseudobrachystachys*/*tigridis, Hordeum marinum/hystrix*, *H. glaucum*, *H. spontaneum*, *Puccinella distans* and *Triticum dicoccoides* (Weiss et al., 2004a, 2004b). Doubt has been cast on the exploitation of a broad spectrum of food plants, however, by Wallace et al.'s (2019) recent analysis of the archaeological context

and purity of archaeobotanical assemblages from pre-agricultural sites. Of the 40-50 genera of grasses represented at pre-agricultural sites across southwest Asia, they find strong evidence (in the form of storage contexts and rich deposits of the same taxon) for the deliberate collection of only 10 grass genera (each of which may represent just one collected species) (Wallace et al., 2019: Table 3). The wild taxa they identified as potential foods include the grass genera, *Avena* (*sterilis*), *Aeluropus*, *Agrostis*, *Alopecurus*, *Bromus*, *Crypsis*, *Hordeum* (*murinum*/*bulbosum*), *Lolium*, *Poa* and *Taeniatherum* (*caput-medusae*), as well as several legume genera (Wallace et al., 2019: Table 4).

It is also widely accepted that there was a narrowing of the plant spectrum in the period leading up to domestication (Weiss et al., 2004b, Willcox et al., 2008, Colledge and Conolly, 2010). It has further been argued that food procurement during the PPNA tends to be characterised by the dominance of wild grasses, including wild cereals, at sites such as Netiv Hagdud (Kislev, 1997), el-Hemmeh (White and Makarewicz, 2012) and Dhra' (Colledge et al., 2018) in the southern Levant, Mureybet (Colledge, 2001), Jerf el Ahmar, Tell Qaramel, Dja'de and Tell 'Abr (Willcox et al., 2008) in the northern Levant, and Hallan Çemi, Demirköy, Qermez Dere and M'lefaat (Savard et al., 2006), Chogha Golan (Weide et al., 2018, Riehl et al., 2013) and Sheik-e Abad (Whitlam et al., 2018) in the eastern region of the Fertile Crescent. Alongside this apparent narrowing of the plant food spectrum, the proportion (by volume) of smallseeded grasses, relative to large-seeded cereals at Levantine sites, apparently also declined from the Middle Palaeolithic, through the Epipalaeolithic to the PPNA (Weiss et al., 2004b).

This predominance of large-seeded cereals has been questioned, however, by Savard et al. (2006) who found that a diversity of plants was exploited at PPNA sites in the eastern region of the Fertile Crescent (Hallan Çemi, Demikröy, M'lefaat and Qermez Dere) and at other PPNA sites in the southern and northern Levant. They concluded that the dietary importance of small-seeded grasses, such as *Aegilops cylindrica/tauschii/speltoides*, *Hordeum murinum* aggregate and *Taeniatherum caput-medusae*, and legumes such as *Vicia/Lathyrus*, *Lens* cf. *orientalis*, *Vicia ervilia* and Trifoliae*/Astragalus*, is often underestimated in this period. This suggests a continued opportunistic approach to the collection of food plants (Savard et al., 2006). Other non-cereal grasses have recently been added to the list of taxa potentially of dietary importance in the eastern region of the Fertile Crescent, such as *Lolium* spp., *Piptatherum holciforme* and *Stipa* spp. (Weide et al., 2018, Whitlam et al., 2018). Based on taxa for which there is contextual and compositional evidence of their deliberate collection as food, Wallace et al. (2019) similarly argue that there was little change in the variety of wild plant foods exploited during pre-agricultural and early agricultural periods (Wallace et al., 2019, p. 13).

In this period the first potential indication of pre-domestication cultivation (the sowing and harvesting of wild crops) is at the Late Natufian site of Abu Hureyra, Syria (Hillman et al., 2001). This is based on an increase in small-seeded legumes (including *Trigonella, Medicago* and *Trifolium* spp.), small-seeded grasses (*Hordeum bulbosum, H. murinum* aggregate and *Eremopyrum* spp.), and species of the Boraginaceae family (including *Arnebia and Buglossoides* spp.), which have been interpreted as probable invaders of cleared, disturbed ground, most likely associated with cultivation (Hillman et al., 2001). Most of the archaeobotanical evidence for pre-domestication cultivation, however, tends to be from the PPNA onwards (Fuller et al., 2012: Table 2, Whitlam et al., 2018, p. 1, Wallace et al., 2019), and similar criteria have been applied at PPNA sites in Syria, where wild species that grow today as weeds in cultivated fields have been used to indicate pre-domestication cultivation at Mureybet (Colledge, 1998). The identification of pre-domestication cultivation has sometimes been based on plant assemblages that contain a significant quantity of wild progenitor seeds that surpass that which could have been gathered from natural stands, as suggested, for example, for the large quantity of wild barley and oat grains found in a granary at the PPNA site of Gilgal, Jordan (Weiss et al., 2006, p. 1609). However, experimental harvesting of stands of wild einkorn in south-eastern Turkey conducted by Harlan (1967) indicates that, over a period of several weeks, more grain may be gathered than a family group could consume in a year, suggesting that large quantities of progenitor species may result from the harvesting of wild stands, prior to any attempt at cultivation.

Archaeobotanical evidence, in the form of wild progenitor abundance and/or the presence of potential weed species, has been used to suggest pre-domestication cultivation at other PPNA sites across the Fertile Crescent, for instance: in the southern Levant at Iraq el-Dubb, Dhra, Gilgal, Nativ Hagdud, Zahrat adh Drha and el-Hemmeh and Jericho (Hopf, 1983, Bar-Yosef et al., 1991, Kislev, 1997, Colledge, 2001, Edwards et al., 2004, Weiss et al., 2006, Melamed et al., 2008, Kuijt and Finlayson, 2009, White and Makarewicz, 2012, Colledge et al., 2018); in the northern Levant at Mureybet, Tell 'Abr, Jerf el Ahmar, Dja'de (Syria) and Çayönü (southeast Turkey) (van Zeist and Bakker-Heeres, 1984, van Zeist and de Roller, 1994, Colledge, 1998, Willcox et al., 2008); and, at one site in the eastern region of the Fertile Crescent, Chogha Golan (Iran) (Riehl et al., 2013). The cultivation of domesticated cereals and pulses arose during the PPNB (Weiss and Zohary, 2011), as evidenced by the presence of non-shattering rachis and increases in grain size (i.e. morphologically domesticated cereals). Some of the earliest, undisputed evidence for domesticated crops has been identified at Ain Ghazal, Jericho, Yiftal 'el and Tell Aswad in the southern Levant, from Abu Hureyra, Cafer Höyük and

Çayönü in the northern Levant, and Jarmo and Ali Kosh in the eastern region of the Fertile Crescent (Zohary et al., 2012: Map 1, see also Nesbitt, 2002).

Savard et al. (2006) observe that, given the relative paucity of large-seeded grasses at preagrarian sites in southwest Asia compared to other species, the inclusion of cereals (einkorn, emmer and barley) amongst the Neolithic founder crops is rather surprising, and the same could be said of the pulse founder crops (lentil, pea, bitter vetch and chickpea). However, although they rarely predominate at Epipalaeolithic and PPNA sites, the plant species collected by pre-agricultural hunter-gatherers include the wild cereal crop progenitors *Triticum baeoticum* (wild einkorn), *Triticum dicoccoides* (wild emmer), *Hordeum spontaneum* (wild barley), and wild pulse crop progenitors *Pisum elatius* and/or *Pisum humile* (wild pea), *Lens orientalis* (wild lentil), *Vicia ervilia* (wild bitter vetch) and *Cicer reticulatum* (wild chickpea) (Zohary et al., 2012). The first clear evidence for domesticated plants in southwest Asia appears at a number of PPNB sites, and, at around 10.4-10.1 kyr cal. BP, the 'Neolithic package' of 'founder' crops was established, which includes the cereal crops, *Triticum monococcum* L. (einkorn wheat), *Triticum dicoccum* Schübl. (emmer wheat) and *Hordeum vulgare* L. (barley), and the pulse crops, *Pisum sativum* L. (pea), *Lens culinaris* Medik. (lentil), *Vicia ervilia* (L.) Willd. (bitter vetch), and *Cicer arietinum* L. (chickpea) (Zohary et al., 2012). These founder crops and their progenitors are listed in Table 2.2. For the sake of brevity, the traditional classifications of cereal and pulse crops and their wild progenitors will be used in the text (following Zohary et al. 2012). The nomenclature for other wild grass species follows the World Checklist of Selected Plant Families (WCSP, 2017) and for other wild legume species follows The Plant List (2013) (see Appendix A for a complete list of all species used in this thesis).

In addition to the known Neolithic 'founder' crops, it has been suggested that several other species may have been domesticated as additional crops at around the same time in the Fertile Crescent (Weiss et al., 2006, Fuller et al., 2012). Fuller et al. (2012: Table 1) list eight species as potential additional early cereal and pulse crops domesticated in southwest Asia. Most of these suggested additional Neolithic crops are not, however, generally accepted (e.g. Abbo et al., 2013a). Four of them, *Secale cereale* L. (rye, progenitor *S. vavilovii* Grossh.), *Avena sativa* L. (oat, progenitors A. *sterilis* L.*/fatua* L.), *Vicia faba* L. (broad bean, progenitor unknown), and *Lathyrus sativus* L. (grass pea, likely progenitor *L. cicera* L.), are extant crops (Zohary et al., 2012). Although it has been suggested that oat (Weiss et al., 2006, Kislev et al., 2010) and rye (van Zeist and Casparie, 1968, van Zeist and Bakker-Heeres, 1986, Hillman, 1975, 2000, Hillman et al., 1989, 2001, Willcox and Fornite, 1999, Willcox, 2002, Willcox et al., 2008, 2009) may have been domesticated early, it is more generally thought that they, and the other extant

crops, were domesticated later and outside the Fertile Crescent (Zohary et al., 2012, Abbo et al., 2013a) and so they are normally considered 'secondary crops'.

The other species on Fuller's list are suggested 'lost crops' resulting from 'false starts' (Weiss et al., 2006, Fuller et al., 2012), that is crops that may have been domesticated at about the same time as the founder crops in the Fertile Crescent but which later fell out of cultivation. Of these, there is no archaeological evidence to support Ladizinsky et al.'s (1983) hypothesis that the large-seeded Western Mediterranean wild black lentil is a feral relic of an early domestication of *Lens nigricans* (Fuller et al., 2012, Abbo et al., 2013a), and *Vicia peregrina* may have been a (possibly toxic) weed of other crops (Melamed et al., 2008, Abbo et al., 2013a). There is more evidence for the early domestication of the remaining 'lost crops' on Fuller's (2012) list, two-grained einkorn (van Zeist and Waterbolk-van Rooijen, 1996, Köhler-Schneider, 2003, Willcox, 2004, 2005; putative progenitor *T. thaoudar* or *T. urartu*) and the 'new' glume wheat (Jones et al., 2000b, Fairbairn et al., 2002, Köhler-Schneider, 2003; putative progenitor *T. araraticum*). The progenitors of these two crops and the 'secondary' cereal crops are listed in Table 2.3, and were included in some of the analyses presented in this thesis.
Chapter 3: Methodology

3.1 Introduction

This chapter presents the criteria for plant species selection (Section 3.2) and the functional attributes selected for measurement, including the ecological significance of the functional traits in relation to the process of domestication, and the protocols for obtaining the plant attribute measurements (Section 3.3). Attribute measurements obtained by the author were from field collections from sites within southwest Asia and southern Europe, and four controlled growth experiments that were conducted within dedicated plant growth facilities at the Department of Animal and Plant Science, University of Sheffield. Details of the field collection sites (used by the author and others), including site location, environment and species collected, are presented in Section 3.4, and the methods used for the four controlled growth experiments in Section 3.5. The methods of statistical analysis applied to the attribute data are described in Section 3.6.

In addition, permission was given to integrate relevant plant trait data from a functional ecological database of field collections of weed species (Jones et al., 1995, Jones et al., 1999, Jones et al., 2000b, Charles et al., 1997, Charles et al., 2002, Charles and Hoppé, 2003, Charles et al., 2003, Palmer, 1997, Bogaard et al., 1999, Bogaard et al., 2001). This database also included data collected by J. Hodgson (University of Sheffield) and M. Hudson (formally University of Sheffield), and access was also granted to relevant plant trait data accrued as part of the Agricultural Origins of Urban Civilization (AGRICURB) Project (Bogaard et al., 2016a, Bogaard et al., 2016b), University of Oxford.

3.2 Species selection

The species selected for study included domesticated cereals and pulses, their wild progenitors and other wild grasses and legumes that were not domesticated. The choice of which species to measure was first and foremost on the basis of archaeobotanical evidence for their likely utilisation at Late Epipalaeolithic and Early Neolithic sites within the Fertile Crescent. Other subsidiary criteria for selection are indicated below as they relate to particular species.

3.2.1 Domesticated cereals and their wild progenitors

Those cereals and pulses that are known to have been domesticated in the Early Neolithic period (the 'founder crops' or 'primary' domesticated species) and their wild progenitors were selected, based on the most up-to-date information available at the time of writing. These

include the six primary domesticated cereal and pulse crops, *Triticum monococcum* (einkorn), *T. dicoccum* (emmer), *Hordeum vulgare* (barley), *Pisum sativum* (pea), *Lens culinaris* (lentil) and *Cicer arietinum* (chickpea), and their wild progenitors, *Triticum baeoticum, T. dicoccoides, Hordeum spontaneum, Lens orientalis, Pisum elatius* and *P. humile* (formerly *P. sativum* var. *pumilio*) and *Cicer reticulatum* respectively (Weiss and Zohary, 2011, Zohary et al., 2012). Two *Pisum* progenitors were selected because both are thought to have contributed to the genepool of domesticated *Pisum sativum* (Smýkal et al., 2010, Zohary et al., 2012). *Vicia ervilia* (bitter vetch), which is also thought to be a founder crop, was not included because of the inability to distinguish wild *V. ervilia* from the domesticated archaeological material (see Butler, 2009).

As well as the primary domesticated crops and their wild progenitors, the wild progenitors of two 'secondary' domesticated species (that were probably domesticated later and outside the Fertile Crescent) – *Avena sterilis* and *A. fatua* (wild progenitors of *A. sativa* – oat) and *Secale vavilovii* (wild progenitor of *Secale cereale* - rye) – were selected for comparison with the progenitors of the primary crops, and with wild species that were never domesticated. Two putative progenitors of possible 'lost crops' (that may have been domesticated in the Fertile Crescent but later fell out of cultivation) were also selected – *Triticum urartu* (possible progenitor of two-grained einkorn – Willcox, 2005) and *T. araraticum* (possible progenitor of the 'new glume wheat' – Jones et al., 2000b) – as well as *T. timopheevii*, which has been suggested as a possible candidate for the identification of the new glume wheat (Jones et al., 2000b).

3.2.2 Other wild grass and legume species

The primary criterion for selection of wild species that were never domesticated was to include those wild grasses and legumes that were found in quantity in secure contexts from Late Epipalaeolithic and/or Early Neolithic sites within the region, using a comprehensive database of archaeobotanical records (Wallace et al., 2019). This database contains archaeobotanical evidence (including plant identifications, abundance and frequency) from over 3000 discreet archaeobotanical samples from 52 sites within southwest Asia (Wallace et al., 2019) (as shown in Figure 2.7). It collates the work of four projects, which, taken together, include all published and some unpublished archaeobotanical reports for Late Epipalaeolithic and PPN sites throughout the Fertile Crescent. These were compiled by Sue Colledge during "The Origin and Spread of Neolithic Plant Economies in the Near East and Europe" project (AHRB, PIs Stephen Shennan and James Conolly, University College London) and the "Domestication of Europe" project (NERC, PI Terry Brown, University of Manchester); and by

Alexandra Livarda and Michael Wallace during the "Origins of Agriculture: an Ecological Perspective on Crop Domestication" project (NERC, PI Colin Osborne, University of Sheffield) and the "Evolutionary Origins of Agriculture" project (ERC, PI Glynis Jones, University of Sheffield).

First, wild species of *Triticum, Hordeum*, *Pisum*, *Lens* and *Cicer* were considered important for comparison with the domesticated and progenitor species of the same genera. Two wild *Triticum* species were already included as putative progenitors of 'lost' crops (Section 3.2.1), and *Hordeum murinum* L. was selected as the most frequently occurring *Hordeum* species in the archaeobotanical database, as was *H. marinum* Huds., which was also represented in the database. *Pisum fulvum* Sibth. & Sm. was selected as the only representative of *Pisum* in the archaeobotanical database, but *Lens* and *Cicer* were represented in the database only by the progenitors of known domesticates. For this reason, two other wild species of *Lens* (*L. culinaris* subsp. *odemensis* (Ladiz.) M.E. Ferguson et.al. and *L. nigricans* (M. Bieb.) Godr.), and a wild form of *Cicer* (*C. judaicum* Boiss.), were selected because they are native to the eastern Mediterranean region (including the Levantine corridor) and, in the case of *L. odemensis,* to Turkey (POWO, 2019).

Other wild species to target for field collections and growth experiments were narrowed down, on the basis of the frequency of the archaeobotanical remains (present in at least 10 samples), to 23 genera: the grasses *Aegilops*, *Alopecurus*, *Bromus*, *Echinaria, Eremopyrum*, *Lolium*, *Phalaris*, *Poa, Setaria, Stipa, Taeniatherum* and *Vulpia*; and the legumes *Astragalus, Coronilla*, *Lathyrus*, *Lupinus*, *Medicago*, *Melilotus*, *Onobrychis, Scorpurius*, *Trifolium, Trigonella* and *Vicia*. Where possible, species-level identifications within these genera were chosen for the field collections and the growth experiments. Larger aggregated groups were also identified, and some of these, such as the small-seeded legumes, Trifolieae and small-seeded grasses, were very common in the archaeobotanical database (32,366 seeds of small-seeded legumes recorded from 14 samples, 2,307 seeds of Trifolieae recorded from 195 samples and 533 seeds of small-seeded grasses recorded from 132 samples). Therefore, where specific identifications were made within these broad categories, these were selected as target species (for example, species of the genera *Hymenocarpos, Lotus* and *Ononis* for small-seeded legumes and *Brachypodium, Digitaria, Echinochloa* and *Eragrostis* for small-seeded grasses).

A secondary selection criterion was to choose species with an annual life history (for direct comparison with the annual domesticated crop and wild progenitor species) rather than biennial or perennial species. Information on life history was extracted from floras for the regions in the Fertile Crescent. For wild taxa that were identified only to genus in the

archaeobotanical record, 'representative' species were chosen on the basis of ecological information on their occurrence, frequency and distribution within the study region, which was also obtained from the relevant floras, notably the Flora of Iraq (Guest and Al-Rawi, 1966, Townsend and Guest, 1968, Townsend and Guest, 1974), Flora Palaestina (Feinbrun-Dothan, 1978, Feinbrun-Dothan, 1986, Zohary, 1966, Zohary, 1972b) and the Flora of Turkey (Davies, 2008). The on-line database Plants of the World Online (POWO, 2019) was also consulted.

3.3 Functional Attribute Selection

3.3.1 Rationale

For the purposes of this research, the functional attributes selected for measurement comprise those that will enable inferences to be made about vegetation responses to potential ecological and anthropogenic selection pressures. Those attributes relevant to vegetation development, in response to past environmental selection pressures (notably climate, soil nutrient and water status), and anthropogenic activities associated with habitat disturbance (such as habitation, animal grazing, early cultivation and soil improvement) were chosen (Table 3.1). Attribute selection and methodology were informed by previous studies that used and developed the functional ecological approach within an archaeological framework (Jones et al., 1995, 1999, 2000b, Charles et al., 1997, 2002, 2003, Charles and Hoppé, 2003, Palmer, 1997, Bogaard et al., 1999, 2001).

3.3.2 Measurement procedures

The protocols for the measurement of the selected functional traits follow those used, and developed, by the weed ecology project within the Department of Archaeology, University of Sheffield (i.e. Jones et al., 1995, 1999, 2000b, Charles et al., 1997, 2002, 2003, Charles and Hoppé, 2003, Palmer, 1997, Bogaard et al., 1999, 2001), and are in line with functional trait measurement protocol handbooks by Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013). Under field conditions, the plants selected for measurement were reproductively mature, robust specimens, located in well-lit environments (preferably totally unshaded), and that had not been severely affected by herbivores or pathogens (Cornelissen et al., 2003, p. 339, Perez-Harguindeguy et al., 2013, p. 171-72). Selection of plants from unshaded locations is particularly important for some leaf traits (such as specific leaf area and leaf thickness), which are known to be plastic in response to light (Shipley, 2002, Cornelissen et al., 2003, p. 339, Hodgson et al., 2011), wherein phenotypic plasticity is the ability of one genotype to produce more than one phenotype when exposed to different environmental conditions

(Garnier et al., 2016). Similarly, plants grown under experimental conditions were also measured when fully mature.

The methodology used includes protocols to encompass potential variation within species, which can be high for certain traits (Garnier et al., 2007, Albert et al., 2011, Perez-Harguindeguy et al., 2013). In particular, all selected traits were measured several times, where possible, for each species, both for the field collections and the experimental plants. For the field collections, every effort was made to replicate attribute measurements for each species at a minimum of three different locations (following Charles et al., 1997, Bogaard et al., 1999, Jones et al., 2000a) and collections were made from different geographical regions (northern Europe, southern Europe and southwest Asia). Collections in the field were made on an encounter basis and, where easily achievable, a larger number of replicate attributes measurements was taken for each species. The number of replicates for the species used in this thesis ranges from 1 to 24. For the experiments, measurements were taken from three to ten different plants for each species. The exact number of replicates measurements for each species was dependant on the capacity of the growth facilities (glasshouses can accommodate more plants than controlled growth chambers), and the success rate of germination and growth to maturity of the plants. The experimental plants were grown from germplasm obtained from at least two different accessions for each species, with accessions selected from locations within the Fertile Crescent, where possible.

3.3.2.1 Attributes relating to the duration and quality of the period for plant growth

Previous research has shown that species attributes relating to the duration and quality of the plant growth period (such as canopy size, leaf size and leaf 'density') tend to be associated with highly fertile habitats (Bogaard, 2004).

3.3.2.1.1 Canopy size attributes

Canopy height is the shortest distance between the ground level and the top of the highest leaf (excluding inflorescences) on a plant (Perez-Harguindeguy et al., 2013). Maximum canopy size provides an estimate of whether or not a species is capable of achieving high biomass, and the maximum size of a species is determined by its growth rate and by the length of its normal period of vegetative growth (Charles et al., 1997, Bogaard et al., 1999, Jones et al., 2000a). It has been shown that species capable of achieving high values for canopy height and/or diameter are characteristic of infrequently disturbed, productive conditions (Charles et al., 1997, Bogaard et al., 1998, 1999, Bogaard, 2004, Jones et al., 2000a). By contrast, those species with consistently smaller canopy dimensions are indicative of one of two situations:

unproductive conditions with infrequent disturbance or productive conditions with frequent disturbance (Bogaard et al., 1998, Bogaard, 2004). Some species are inherently smaller because they exploit less productive conditions where factors such as nutrients, water, light and temperature limit the quality or length of the growth period, and attain their size by prolonged but relatively slow growth which can only be achieved if disturbance is infrequent (Charles et al., 1997, Bogaard et al., 1998, 1999, Jones et al., 2000a). The other group of smaller weeds exploits highly productive but severely disturbed sites – although fast growing, such plants achieve at best medium size at maturity, but this enables them to complete their life cycle before the next disturbance event (Jones et al., 2000a).

Canopy height and diameter (cm) were measured at one to five locations for the field collections on an encounter basis (following Bogaard et al., 1999), and for three to ten experimental plants (the glasshouses can accommodate more plants). Canopy measurements were taken towards the end of the growing season, when the plant was fully mature and in flower.

3.3.2.1.2 Leaf size and density attributes

Leaf area. Leaf area (LA) is defined as the one-sided or projected area of an individual leaf (mm²) (Perez-Harguindeguy et al., 2013, p. 189), and is an easily measured and widely studied ecological variable that corresponds with habitat quality (Hodgson et al., 2017). This is because, under fertile conditions, there is greater investment of acquired resources into leaves (and roots) in order to maximise light interception and nutrient acquisition (Hodgson et al., 2017, p. 2). Put simply, increased fertility is generally associated with larger leaves. Conversely, species characteristic of less favourable habitats, due to soil nutrient status, water availability and/or climate, tend to have small leaves (e.g. McDonald et al., 2003, Hodgson et al., 2017, Santini et al., 2017). Furthermore, under fertile conditions, large leaves in combination with a tall and extensive canopy promote competitive exclusion (Keddy et al., 2002, Hodgson et al., 2017). For the purposes of this research, this leaf trait is used to calculate specific leaf area and the ratio of leaf area to thickness (see below).

Specific leaf area. Specific leaf area (SLA) is leaf area (mm²) divided by its dry mass (mg) (Charles et al., 1997, Cornelissen et al., 2003, Perez-Harguindeguy et al., 2013). Charles et al. (1997, p. 1152) identify SLA as the most easily measured trait of a number of important structural and functional characteristics, including net photosynthetic capacity, growth rate, leaf life-span and toughness, all of which are strongly correlated with habitat productivity and the capacity for rapid growth (Reich et al., 1992, 1999, Poorter and De Jong, 1999, Ordoñez et al., 2009, Violle et al., 2009). In general, species in permanently or temporarily resource-rich

environments tend to have higher SLA than those in resource-poor environments, although there can be considerable variation in SLA among co-occurring species (Perez-Harguindeguy et al., 2013). Drawbacks have been identified when using SLA as an indicator of productivity (Hodgson et al., 2011), as it is very variable between replicates and significantly influenced by leaf thickness (Wilson et al., 1999), and responds strongly to variation in environmental conditions and light levels (Shipley and Almeida-Cortez, 2003, Hodgson et al., 2011). Nevertheless, it has been shown that species ranking using SLA is sufficiently stable, despite spatial and temporal variability, to use this trait in plant classifications (Poorter and De Jong, 1999, Garnier et al., 2001). Due to the plasticity of SLA, the use of this trait in combination with other productivity traits (such as DMC) is advocated (Garnier et al., 2001, Hodgson et al., 2011).

Leaf area:leaf thickness. This trait is the maximum leaf area per node (mm²) divided by the mean leaf thickness (mm) (Bogaard et al., 1999, Jones et al., 2000a). The ratio of leaf area to leaf thickness may also distinguish species of productive habitats (with small, thin leaves, or large, thick leaves) from those of unproductive habitats (with small, thick leaves) (Jones et al., 2000a, Charles et al., 2003).

Leaf dry-matter content: Leaf dry-matter content (DMC) is the dry mass (mg) of a leaf divided by its fresh mass (g) (Bogaard et al., 1999, Cornelissen et al., 2003, p. 345, Perez-Harguindeguy et al., 2013, p. 190), and is expressed as a percentage (dry weight x 100/fresh weight) (Bogaard et al., 1999). DMC describes the amount of dry matter investment in leaves (Bogaard et al., 1999). The combination of leaf traits SLA and DMC reflects the 'trade-off' between resource acquisition (typically high SLA/low DMC) and resource conservation (typically low SLA/high DMC) (Reich et al., 1992, Lavorel and Garnier, 2002, Díaz et al., 2004, Ordoñez et al., 2009). This acquisition-conservation trade-off distinguishes between two main functional strategies: exploitative species and conservative species (Albert et al., 2010). Exploitative species are characterised by high SLA, low DMC (thin leaves), high photosynthetic and high growth rates, and are proficient competitors in fertile, disturbed habitats (Grime et al., 1997, Reich et al., 1999, Garnier et al., 2007, Albert et al., 2010). Conversely, conservative species are characterised by low SLA, high DMC (thick leaves), low growth rates and high resource conservation, and are adapted to growth in low fertility conditions (Grime et al., 1997, Reich et al., 1999, Garnier et al., 2007, Albert et al., 2010). In terms of trait plasticity, DMC has an advantage over SLA in terms of indicating productivity, because fast-growing species of productive habitats have low DMC irrespective of whether they are shaded by other plants, or whether they occur in well-illuminated situations with thicker leaves (Bogaard et al., 1999, Hodgson et al., 2011).

Following Pérez-Harguindeguy et al. (2013, p. 186), leaves that were relatively young but fully expanded (and presumably more photosynthetically active) from adult plants, were selected from species targeted for measurement (including leaf area, leaf width, leaf thickness and fresh/dry leaf weight). As leaf thickness and SLA can vary within the canopy (Pérez-Harguindeguy et al. 2013), leaves were collected from the upper, middle and lower parts of the canopy, in order to capture the variability within the canopy (and therefore individual plants, *sensu* Albert et al., 2010, p. 1194). The leaves were wrapped in moistened tissue paper in order to ensure rehydration and avoid shrinkage of leaves. The leaves were kept in sealed plastic bags and stored in the dark in a cool box (notably field collections) or refrigerator prior to measurement (following Bogaard et al., 1999).

To measure these fresh leaf traits, the fresh leaves were gently patted dry, their watersaturated fresh mass was measured and then the leaves placed on a flatbed scanner; leaf area was measured using the image analysis software programme Leafarea (A. P. Askew, University of Sheffield, UK). Five leaves per collection (variously from upper, middle and lower parts of the plant), including largest leaf, were measured individually. Large leaves, that exceeded the area of the flatbed scanner, were cut into smaller pieces for ease of measurement. Leaf thickness was measured as the inter-veinal thickness (to the nearest 0.01 mm) using a dial thickness gauge (micrometer) (Bogaard et al., 1999), at one point (for the field collections) or three points (for the experimental plants) per leaf blade, for three to five leaves per field collection/experimental plant, and the mean then calculated for each collection/plant. When all of the measurements were complete, leaf material was placed in envelopes and dried at either 70°C for 72 hours or 80°C for 48 hours (depending on study/data source). Once dried, the leaf material was placed in a desiccator with silica gel until ready for weighing. Where the collection comprised several tiny leaves, they were weighed together as one, then the weight was divided by the number of leaves in order to improve the accuracy of weighing. The mean value was calculated from the results for the different collections/experimental plants for each species per experiment/treatment.

3.3.2.2 Attributes relating to water use

It is expected that species with fewer numbers of large stomata will have large genomes (nuclear DNA content), due to the positive correlation of genome size and epidermal cell size (including stomatal guard cells) (Beaulieu et al., 2008, Knight and Beaulieu, 2008). Thereby large genomes are often associated with large epidermal cells, and thus stomata (Beaulieu et al., 2008, Knight and Beaulieu, 2008). Species with larger genomes and corresponding lower numbers of larger stomata will, therefore, show less specialisation for drought avoidance or drought tolerance, than those with many more, smaller stomata, which will also tend to have smaller genomes (Beaulieu et al., 2008, Knight and Beaulieu, 2008). Species with large genomes may indicate cool season peak growth (summer drought avoidance), and those with small genomes may indicate warm season peak growth (i.e. winter annuals versus summer annuals) (Grime & Mowforth, 1982; Grime et al., 1985; Hodgson et al., 2010), which is attributed to the sensitivity of cell division to low temperatures (Grime and Mowforth, 1982, Grime et al., 1985, Bennett and Leitch, 2005, Hodgson et al., 2010).

Genome size has been shown to correlate weakly but positively with seed size (mass) (Jones and Brown, 1976, Marañón and Grubb, 1993, Knight and Ackerly, 2002, Knight et al., 2005, Beaulieu et al., 2007, Hodgson et al., 2010) and a key functional trait of domesticated species and wild crop progenitors is that they tend to be large-seeded (Kluyver et al., 2013, Cunniff et al., 2014, Preece et al., 2015, 2017, 2018). It is therefore anticipated that the (large-seeded) domesticated crops and wild progenitors will tend to have larger genomes than other wild species that may have been utilised by early plant gatherers/agriculturalists (notably smallseeded species), and as such will have comparatively poor water-use efficiency (favouring moist soil conditions), and may also be predisposed to cool season of growth (to achieve summer drought avoidance).

3.3.2.2.1 Stomatal density and size

Stomata are small pores in the leaf surface, each bounded by two guard cells, and provide the principal mechanism controlling the exchange of gases, particularly the influx of carbon dioxide (CO₂) and the efflux of water vapour, between the interior of the leaf and the atmosphere (Hetherington and Woodward, 2003, Lawson, 2009, Hodgson et al., 2010). As such, they are important gates regulating water loss, and the availability of water and $CO₂$ for photosynthesis, which can affect growth and reproduction (Milla et al., 2013). In terms of gaseous exchange and control of water loss, small stomata afford greater water-use efficiency in dry habitats due to their more rapid opening and closure (Hodgson et al., 2010). Conversely, in cool, moist and shaded habitats (where water loss is a less constraining factor), large stomata may be advantageous (Hodgson et al., 2010), in order to maximise gaseous exchange, and in turn resource acquisition.

Leaf material was collected from mature, healthy plants in unshaded habitats (as described in Section 3.3.2.1.2). Three replicate leaves for each field collection/experimental plant were taken from the upper, middle and lower parts of the canopy in order to capture the variability within the canopy (*sensu* Albert et al., 2010, p. 1194). Acetate impressions were taken from the upper and lower surfaces of each leaf (following Beerling and Chaloner, 1992), whereby the leaf surface was covered liberally with acetone and a piece of acetate film was pressed

firmly on top to form impressions of the epidermal cells (Charles et al., 1997). Each leaf impression was examined either at x 400 or at x 100 magnification, and the numbers of stomata in the field of view were counted and the lengths (microns) of at least three closed stomata measured from each leaf impression. In order to obtain stomatal counts and lengths for the experimental plants, photographs of the epidermal impressions were taken (using micropublisher 5 camera in combination with an Axioskop microscope), which were examined using imaging software (ImagePro Insight). Means per individual collection/plant for stomatal density and length were then calculated, as well as per species by geographic region and experimental source.

3.3.2.2.2 Genome size

Genome size refers to the nuclear DNA amount of an organism and is estimated by the total amount of DNA contained within a single (i.e. haploid) set of its chromosomes (Bennett and Leitch, 2005), which is referred to as its 'C-value' (Swift, 1950, Bennett and Leitch, 2005). Cvalues (i.e. estimates of absolute DNA mass) are measured in picograms (pg), where 1 pg = 10^{-1} $12g$ (Bennett and Leitch, 2005, p. 90). Genome size impacts on cell volume (Hodgson et al., 2010), due to the fact that nuclear DNA also has structural, non-genic (non-coding), functions (Bennett, 1972, Cavalier-Smith, 2005) and can therefore indirectly influence cell volume by the physical-mechanical effects of its mass (Bennett, 1972). The strength of correlations between genome size and stomatal guard cell length and epidermal cell area is strong (Knight and Beaulieu, 2008), and epidermal cell area and guard cell length has been shown to scale positively with genome size in angiosperms (flowering plants) (Beaulieu et al., 2008, Knight and Beaulieu, 2008, Hodgson et al., 2010) and negatively with stomatal density (Beaulieu et al., 2008, Knight and Beaulieu, 2008). In other words, across a wide range of major taxa there is a strong correlation: as genome size increases, so does epidermal cell area and guard cell length, which corresponds with a decrease in stomatal density (Beaulieu et al., 2008, Knight and Beaulieu, 2008). This has important ecological implications in terms of species' life-history strategies and resource-use efficiency (Beaulieu et al., 2008), and whether a species is genetically predisposed to thrive in certain environmental conditions. This is because the larger the genome, the larger the epidermal cell size (including stomatal guard cells), which is associated with decreasing stomatal density, and which therefore affects water-use efficiency (Beaulieu et al., 2008). For instance Knight and Ackerly (2002) have demonstrated that largegenome species are not well represented in environments characterised by low precipitation and high temperatures, which are conditions that species with small genomes and many, small stomata (i.e. better water-use efficiency) are physiologically and morphologically better adapted to.

Genome size amount can also be used to predict phenology (season of growth) (Bennett, 1971, Grime and Mowforth, 1982, Grime et al., 1985, Macgillivray et al., 1995). In general, species whose growth peaks in summer tend to have a small genome, while species that grow mainly in the spring tend to have large genomes (Grime and Mowforth, 1982, Grime et al., 1985); this is considered to relate to the sensitivity of cell division to low temperatures, whereby species with large genomes grow early in the spring predominantly through the expansion of cells that had divided in the preceding year, while small-genome species growing in the summer did so by normal cell division (Grime and Mowforth, 1982, Grime et al., 1985, Bennett and Leitch, 2005, Hodgson et al., 2010). However, predicting seasonal growth based on genome size is problematic for annual species (Charles et al., 1997). This is due to the fact that annuals tend to have small nuclear DNA amounts but despite this may achieve large cell size by endopolyploidy (Nagl, 1976, Olszewska and Osiecka, 1984, Leitch and Dodsworth, 2017), which is a process where chromosomes replicate without division of the cell nucleus (Leitch and Dodsworth, 2017). However, within the more 'intermediate' range of genome size (as defined by Soltis et al., 2003, pp. 1196-1197, and see below), large genomes may still be favoured in the cold where cell expansion is a more efficient way of growth than cell division (Bennett and Leitch, 2005), for reasons stated above.

The majority of the estimates of C-values, using haploid C-values (referred to as 1C DNA values), were compiled by J Hodgson from the Plant DNA C-values database maintained at the Royal Botanic Gardens, Kew (Bennett and Leitch, 2012), and supplemented by the author from the same source (Bennett and Leitch, 2012). For the analyses, species were assigned to genome size classes using non-logged transformed 1C-DNA species values, following Soltis et al. (2003), with the classes defined as: very small (<1.4 pg); small (1.4-3.5 pg); intermediate (>3.5-<14 pg); large (14-35 pg); and very large (>35 pg) (Soltis et al., 2003, pp. 1596-1597).

3.4 Field collections

3.4.1 Rationale

Two field collections were made by the author: one collection from a location within the Fertile Crescent in Iraqi Kurdistan; and one in Haute Provence, southern France. These collections followed procedures previously used when constructing functional ecological databases of plant species from Europe and southwest Asia (e.g. Charles et al., 1997, Bogaard et al., 1999, Jones et al., 2000a) as follows, and so are comparable with these earlier collections (outlined in section 3.3.2). Every effort was made to make field collections at the optimum time for measurement in terms of the developmental stage of the plants (i.e. the

flowering/fruiting growth stage). As only specific species were targeted for measurement, collections were made on an 'encounter' or random basis within each collection site. Once a target species had been identified, an individual plant was selected for measurement, ensuring that it was a robust, well grown plant that was located in a well-lit environment and which was not strongly affected by herbivores or pathogens (Cornelissen et al., 2003, p. 339). The functional attributes that could be measured in the field were accordingly taken (i.e. 'whole plant' trait measurements) and additional plant material gathered for laboratory-based measurements (i.e. fresh leaf material). The location, date of collection and any field observations (weather, character of the site, soil-type and evidence for disturbance etc.) were recorded and a photographic archive of the site made. A herbarium specimen was then collected for archive purposes and to aid in identification (which could be completed at a later date and in consultation with a botanist if necessary).

In addition, trait data was used from functional ecological databases of previous field collections from Europe and southwest Asia. Where possible, these data were based on up to five collections of each species from each geographic location, supplemented by plants from botanical gardens and plants that were 'grown-on' from seed obtained from field collections.

3.4.2 Iraqi Kurdistan field collections

Field collections in southwest Asia were made by the author within the Sulaimaniyah province, Kurdistan Regional Government, Iraq. This field trip took place between 15th March and 25th April 2012 and was in conjunction with the Central Zagros Archaeological Project (CZAP), (AHRC, PI Roger Matthews, University of Reading), which was conducting excavations at a Neolithic settlement mound, located within the vicinity of the present rural farming village of Bestansur (see Matthews et al., 2016). The attribute data for these collections are presented in Appendix B.

3.4.2.1 Location

Sulaimaniyah province falls within the mountain region (between 500 and 1800 m a.s.l.) of northern Iraq (Guest and Al-Rawi, 1966) and Bestansur is situated on the fertile Shahrizor, a plain stretching from the north-west to the south-east along the western edge of the Zagros and south-east of Sulaimaniyah between Arbat and Halabja (Altaweel et al., 2012) (Figure 3.1). Iraqi Kurdistan falls within the Csa Köppen-Geiger climate classification and experiences warm and temperate climates, associated with hot, dry summers and cool, wet winters that last from October to May (Altaweel et al., 2012). The land around Bestansur is predominantly a gently sloping agricultural plain, which presently makes up the main cultivation land in this area, with the surface of the landscape composed of slightly undulating thick alluvial sediments

recharged principally by the direct infiltration of rainfall (Maran and Stevanovic, 2009, cited in Elliott et al., 2015).

Sulaimaniyah province is situated within the forest zone, which is characterised by extensive and more or less open (but often largely destroyed) oak forest, with high summer pasture (Guest and Al-Rawi, 1966, p. 2). The collection sites lie on vertisols (Figure 3.2a); typically forming on level or mildly sloping ground in areas with distinct wet and dry seasons, the natural vegetation of vertisols is predominantly grass, savannah, open forest or desert shrub (USDA and NRCS, 1999, p. 784). Vertisols are clayey soils, which display evidence for strong vertical mixing of the soil particles via distinctive cracks that develop over many seasons of wetting and drying (USDA and NRCS, 1999, pp. 783-84). This region in northern Iraq does experience distinct wet and dry seasons, as illustrated in Figures 3.2b and 3.2c, which shows the mean monthly precipitation for Bestansur in January (100-150 mm) and July (less than 20 mm). Whilst the soils are high in nutrients, these climatic characteristics therefore mean that agriculture is only possible with painstaking management (USDA and NRCS, 1999). Guest and Al-Rawi (1966, pp. 2, 72) also note that the annual rainfall, in combination with the arid summers, means that, even in the mountain regions, irrigation is necessary for the success of the crops during the summer months.

3.4.2.2 Collections

In total 30 plant collections were made (Table 3.2), which consisted of functional measurements and herbarium specimens for each species collected, and some replicate species from different habitats. Collections were made from the three distinct physical zones around Bestansur (as identified by Elliott et al., 2015): from Bestansur Neolithic settlement mound (35°22'36.7" N, 045°38'44.4 E, *ca.* 550m a.s.l.) located in the river catchment area; from two fields to the west and south of the Neolithic settlement mound (ascribed 'west field' and 'south field'), in which winter-sown wheat and barley were being grown on the edge of the fertile alluvial plain; and several collections within the limestone toe slopes of the foothills of the Central Zagros mountain range, located to the northeast of Bestansur (Figures 3.3 and 3.4). Figure 3.5 shows the three collection sites in the toe slopes of the foothill collections: 'hill top' (35°24'55.2" N, 045°38'38.9 E, *ca.* 715m a.s.l.); 'mid-slope terrace' (35°24'56.8" N, 0.45°38'30.1" E, *ca* 668m a.s.l.); and 'bottom of slope' (35°24'58.8" N, 0.45°38'37.9" E, *ca* 692m a.s.l.). The vegetation encountered in the different collection sites was varied, as illustrated in Figures 3.6-3.8.

Unfortunately, it was not possible to take the full suite of functional measurements for many of the collections because the development stages of the plants encountered were too early.

Despite six weeks in the field, the late start to the spring season in 2012 meant that the grasses and legumes were only just approaching the appropriate growth stage for measurement purposes (i.e. flowering and fruiting) towards the very end of the field trip. Formal confirmation of the identification of a number of the collections remains outstanding. For the purposes of the analyses, however, these collections could still be included in those analyses using individual collections when coded by family (grasses versus legumes) and domestication status (domesticated, progenitor or wild species, as for analyses in Chapter 4, section 4.1). Those collections that require final identification could not be included in the species attribute means for the Near East field collections (see section 3.7.1). In addition, three collections that were not formally identified whilst in the field were subsequently identified as perennial species (collections 7 and 8, *Poa bulbosa* L., and collection 24, *Hordeum bulbosum* L.), and therefore are not included in the analyses.

3.4.3 Haute Provence field collections

Field collections were made also in Haute Provence, south-eastern France, in conjunction with the Agricultural Origins of Urban Civilization (AGRICURB) Project, University of Oxford (PI Amy Bogaard). In May 2013 the AGRICURB project conducted a preliminary floristic survey of the weeds in crop fields in the region, in advance of the full transect survey planned for June and July 2013 (see Bogaard et al., 2016a), alongside which collections were made of target species for this study.

3.4.3.1 Location

The southern European study area for the AGRICURB project lies within a region of Haute Provence, south-eastern France. This region is defined by the limestone massifs of Mont Ventoux (the region's highest peak, 1912 m (Blondel et al., 2010, p. 103)) and the Montagne de Lure in the north, and the Lubéron massif in the south (Bogaard et al., 2016a) (Figure 3.9). The region includes two calcareous plateaux (Sault and Albion) at c. 800-1000 m altitude to the south-east of Mount Ventoux, and a more varied 'molasse' geology and fractured topography in the northern Lubéron (c. 500-700 m) (Bogaard et al., 2016a). The study area is situated in a transitional climatic position between the semi-humid Mediterranean coast to the south of the Lubéron range, and the oceanic/continental conditions experienced to the north (see Blondel et al., 2010, Figure 1.2, Bogaard et al., 2016a), where Mont Ventoux denotes the limits of the Mediterranean bioclimate in this region (Blondel et al., 2010). In Köppen-Geiger climate classification terms the Sault area is temperate and humid, with warm summers (Cfb), while the northern Lubéron area around Apt is temperate with dry, warm summers (Csb) (Figure 3.9). In the northern area of the study region, the average annual precipitation around Sault is

c. 900 mm, and rainfall remains high year-round, with peaks in October and May (Bogaard et al., 2016a). To the south, around Apt, the average annual precipitation is c. 700 mm and the rainfall follows a more Mediterranean pattern, being distinctly higher in winter (peaking in October and February) than summer (Bogaard et al., 2016a).

The surveys were conducted on crop fields near Sault (c. 800 m altitude), Saint-Christol (c. 800- 1000 m), and Murs (c. 500 m) in the Vaucluse, and near Vachères (c. 700m) and Montfuron (c. 500 m) in Alpes-de-Haute Provence (Figure 3.9) (Bogaard et al., 2016a).

3.4.3.2 Collections

Within the region of Haute Provence, the AGRICURB project targeted organic cereal farming sites (being managed without chemical fertilisers or herbicides), due to the fact that they often include crop varieties adapted to (stony) low-nutrient soils that were managed through crop rotation, with little or no manuring (Bogaard et al., 2016a). It was noted by Bogaard et al. (2016a) that this included a local variety of einkorn wheat, which was typically autumn-sown (normally in October) and had the longest growing season, ripening in August and sometimes September.

In total 72 collections were made on an encounter basis, within the framework of the floristic survey (Table 3.3), from the site locations near Sault, Saint-Christol, and Murs in the Vaucluse, and near Vachères and Montfuron in Alpes-de-Haute Provence. The collections tended to be of species growing in the field verges, which were at the reproductive growth stage, typically in advance of the crops (Figures 3.10 and 3.11). Trait measurement protocols follow those used in earlier projects and outlined in section 3.3.2.

3.4.4 Additional functional attribute data

3.4.4.1 Rationale

To supplement data from the field collections (described in Sections 3.4.2 and 3.4.3), access to functional trait measurement data accrued from previous floristic surveys was granted. These data were principally extracted from a functional ecological database that was created and developed by researchers within the University of Sheffield (PIs Glynis Jones and Mike Charles, PDRAs Amy Bogaard and Carol Palmer), Department of Archaeology, and John Hodgson, Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield). The functional ecological database also includes trait data collected by M. Hudson from collection sites in southern Europe, southwest Asia and botanical gardens in France and Germany. Relevant trait data generated from more recent floristic surveys, carried out as part of the Agricultural Origins of Urban Civilisations project (PI Amy Bogaard), was also made

available for inclusion. Trait data collated by J. Hodgson, which is pertinent to the functional ecological database (notably relating to genome size), was also made available.

3.4.4.2 Functional ecological database

The functional ecological database comprises functional trait measurements primarily resulting from a series of modern surveys of weed floras, developed under traditional husbandry regimes in southern Europe (including Spain and Greece) and southwest Asia (Jordan), as discussed in Section 2.4.3 (see Jones et al., 1995, 1999, 2000a, Charles et al., 1997, 2002, 2003, Charles and Hoppé, 2003, Palmer, 1997, Bogaard et al., 1999, 2001). This database also includes trait measurements personally collected by J. Hodgson and M. Hudson, together with genome size data extracted by J. Hodgson (see Section 3.3.2.2.2). Functional trait measurement protocols were developed for this project as outlined in Section 3.3.2.

The inclusion of species from this functional ecological database enabled the incorporation of a wider range of annual grass and legume species than were encountered by the author during the field trips to Iraq and France (Sections 3.4.2 and 3.4.3). Trait data for target species collected in northern Europe, southern Europe and the southwest Asia were extracted, equating to 759 individual collections (Table 3.4). These data also include trait measurements from collections made by M. Hudson in Spain, Israel and Palestine, and from four botanical gardens: the Botanical Garden of Caen, Normandy, France; Leuven Botanic Garden, Belgium; Leipzig Botanical Garden, Germany; and Leibniz Institute for Plant Genetics and Crop Plant Research (IPK), Gaterslaben, Germany (collection trips 20 – 24, Table 3.4). The abstracted data collected by J. Hodgson relate to plant material collected from unshaded habitats primarily in northern and southern Europe, with some from collections in southwest Asia (Hodgson et al., 2011). In addition, some traits were measured from species 'grown-on' within the UK using seed obtained from field collections within Europe and southwest Asia (collection trips 65, 69, 91, 114) (Table 3.4).

3.4.4.3 AGRICURB Data

In addition to the trait measurement data for the 72 collections from the Haute Provence trip (outlined in Section 3.4.3), trait data from 22 field collections were extracted from the final dataset for the Agricultural Origins of Urban Civilisation project (PI Amy Bogaard, University of Oxford, with the involvement of Michael Charles, University of Oxford, Glynis Jones and John Hodgson, University of Sheffield) (Table 3.5). These data were also derived from floristic surveys of crop fields in Haute Provence (see Bogaard et al., 2016a). Measurement protocols followed those developed for earlier projects as outlined in Section 3.3.2.

3.5 Controlled growth experiments

3.5.1 Rationale

The benefit of obtaining trait measurements from natural habitats is that they provide attribute values from plants that have been subject to complex abiotic and biotic interactions within the vegetation community, compared to the often 'optimised' growth conditions of laboratory grown plants (Garnier and Freijsen, 1994, Poorter et al., 2016). For the purposes of this research, however, the benefits of conducting laboratory-based growth experiments are that they enabled the control of the growth conditions, as well as the surety of obtaining measurements from the target species. Growth experiments can allow the replication of (past or predicted) environmental conditions that cannot be achieved under current natural conditions, and also facilitate greater opportunities for observation and measurement during the development of the plants, which would not necessarily be afforded when making field collections.

An important consideration in the development of the functional-based model for this research is that atmospheric carbon dioxide partial pressure ($pCO₂$) during the Late Epipalaeolithic and Early Neolithic periods was lower than present-day levels. The Younger Dryas stadial (c. 12.9-11.5 kyr cal. BP), which occurred during the Late Epipalaeolithic, resulted in a decline in temperature and water availability (Bogaard and Whitehouse, 2010) and marked the beginning of the post-glacial rise in global $pCO₂$ levels from 18 Pa (glacial) to 27 Pa (post-glacial) (Cunniff et al., 2010). Hypotheses proposing that *p*CO₂ was a global limiting factor for the domestication process (Sage, 1995, Richerson et al., 2001) have been supported by recent experimental research (Cunniff et al., 2008, 2010, 2017). The results of this experimental research have also indicated that the post-glacial increase in $pCO₂$ could have conferred a competitive advantage on the crop progenitors compared to other wild species that were potentially available and utilized by early agricultural societies (Cunniff et al., 2008, 2010, 2016, 2017). It will, therefore, be important to determine if and how past climate conditions during these pre-/early cultivation periods may have acted on the traits and species selected for this research, as this will affect the predictive ability of the functional-based model.

Plant trait measurements were obtained from four growth experiments conducted at dedicated plant growth facilities within the Department of Animal and Plant Sciences, University of Sheffield. Two growth experiments were conducted specifically for this study, and two were conducted for the Origins of Agriculture (OA) project, from which access to

specific plant trait measurements (as outlined above) was granted. The attribute data for the four growth experiments are presented in Appendix B.

3.5.2 2013 Glasshouse experiment

3.5.2.1 Plant material

Along with the established founder cereal and pulse crops from the Fertile Crescent and their wild progenitors, the selection of other wild species was informed by the archaeobotanical database (Wallace et al., 2019). Consideration was also given to the measurement of plants with a range of seed sizes, with target species including both large-seeded and small-seeded wild annual grass and legume species. In addition, several species were included for comparison where archaeobotanical evidence suggests that they may have been domesticated in the Fertile Crescent, but are no longer cultivated: *Triticum araraticum*, a potential progenitor of the new glume wheat (Jones et al., 2000b) and *T. urartu*, a potential progenitor of domesticated two-grained einkorn (Willcox, 2005). In total, 20 grass species and 20 legume species were selected, with between one and five accessions per species (Tables 3.6 and 3.7 respectively).

Seed material was obtained from the National Plant Germplasm System (United States Department of Agriculture, Beltsville, MD, USA), the John Innes Centre Germplasm Resources Unit (Norwich, UK), the Millennium Seed Bank (Kew Gardens, Wakehurst Place, UK) and IPK Gaterslaben Genebank (Stadt Seeland, Germany), and included seed from accessions grown-on from the 2012 chamber experiment (see Section 3.5.5.1). Where possible, accessions from southwest Asia (including the Fertile Crescent) were selected.

3.5.2.2 Growth conditions

Seeds were prepared by removing the outer glumes (where necessary) and the legumes were scarified with sandpaper to break seed dormancy. Prior to planting, the fresh seed mass of individual seeds was measured. Seeds were germinated during March 2013, in batches of 20 seeds in trays containing plastic inserts with a 1:1 mixture of John Innes no. 2 compost (LBS Garden Warehouse, Lancashire, UK) and Chelford 52 washed sand (Sibelco UK Ltd, Sandbach, UK) (Preece et al., 2015). The choice of the sand and compost (7 parts loam, 3 parts peat, 2 parts sand, N:K:P = 20 : 10 : 10) growth mix followed previous plant domestication growth experiments (Cunniff et al., 2008), where attempts were made to replicate an unimproved soil (following Ivandic et al., 2000). The growth medium was saturated with water and seeds were placed in rows to enable individuals to be identified throughout germination (Preece et al., 2015).

The trays were placed in a controlled-environment growth cabinet (Conviron BDW 40, Conviron, Winnipeg, MB, Canada) with conditions set to approximate the growing season for winter annuals in the Fertile Crescent (Preece et al., 2015). The temperature was set to 20/10°C (day/ night), an 8 hour photoperiod and photosynthetic photon flux density (PPFD) of 300 μ mol m⁻²s⁻¹ (Preece et al., 2015). In order to stimulate flowering the seedlings were subject to a 6-8 week vernalization treatment; following germination, once the seedlings reached the two-leaf stage, they were transferred to a second cabinet at a constant temperature of 4° C (with the same light regime). On completion of the vernalization treatment, in July 2013, the plants were moved to a glasshouse (Arthur Willis Environment Centre, University of Sheffield, UK), where individual seedlings were planted into 11 litre square pots (20 x 20 x 25 cm), again with a 1:1 mixture of John Innes no. 2 compost and Chelford 52 washed sand. Consideration was given to avoid restriction of root growth and the large pots greatly exceeded the recommended minimum soil volume (1 litre for each 2 g of dry plant mass) to avoid restriction of root growth in comparative experiments (Poorter et al., 2012, Preece et al., 2015). The temperature in the glasshouse was maintained at 24/15°C (day/night) and was naturally sunlit during the high-light conditions of summertime (Preece et al., 2015).

3.5.2.3 Experimental design and measurements

Two glasshouse rooms were used, with a randomised block design and ten blocks in total, with one individual of each species per block (allowing ten replicates per species) (Figure 3.12). Plants were watered three times per week and given Long Ashton nutrient solution (50% concentration) at two points during the growing period (Preece et al., 2015). After two months of growth, at maturity, plant trait measurements were taken, with between three and eight replicates per species. Fresh leaf material was collected for fresh leaf trait measurements (including SLA, DMC, as described in section 3.3.2.1.2) and for leaf epidermal traits (stomatal length and density, as outlined in section 3.3.2.2.1). Records of canopy height and diameter were mislaid, following the experiment, and so are not available for analysis.

3.5.3 2013 Controlled growth experiment

Partial pressure of CO₂ (pCO₂) has been suggested as a global limiting factor in the process of domestication (Sage, 1995, Richerson et al., 2001). Previous research involving plant growth experiments conducted under glacial (18 Pa) and post-glacial (\approx 27 Pa) CO₂ levels, support the $CO₂$ -limitation hypothesis, having demonstrated that atmospheric conditions of the last glaciation would have placed direct and indirect restrictions on productivity of crop progenitors (Cunniff, 2009, Cunniff et al., 2008, 2010, 2016, 2017). This experiment was designed to determine whether or not the traits selected for the purposes of this research,

behaved similarly under reduced pre-domestication cultivation $CO₂$ levels (~24 Pa) compared with current ambient CO₂ levels (∼38 Pa). The aim of the experiment was therefore to ascertain whether measurements of traits in crops, crop progenitors and wild species grown under modern ambient $CO₂$ (~38Pa) levels (both in the field and experimentally) differ from those in plants grown under pre-domestication $pCO₂$ (~24 Pa) levels. This will enable an assessment of whether interpretations made about species and selection pressures in relation to domestication status are still applicable under past CO₂ levels.

In order to address these aims, a subset of species was selected for growth under reduced $CO₂$ conditions, including established founder cereal and pulse progenitor species from the Fertile Crescent, and a range of large- and small-seeded wild grass and legume species used in the 2013 glasshouse experiment (see Section 3.5.2).

3.5.3.1 Plant material

Plants selected for this experiment comprise 15 grass species and 15 legume species grown under two CO₂ levels, in order to replicate pre-domestication CO₂ (~24 Pa) and current ambient $CO₂$ (~38 Pa) conditions. The species included wild cereal and pulse progenitors, and wild grasses and legumes (Tables 3.8 and 3.9 respectively), including both small and largeseeded species. Seed material was obtained from the National Plant Germplasm System (United States Department of Agriculture, Beltsville, MD, USA), the John Innes Centre Germplasm Resources Unit (Norwich, UK), the Millennium Seed Bank (Kew Gardens, Wakehurst Place, UK) and IPK Gaterslaben Genebank (Stadt Seeland, Germany), and included seed from accessions grown-on from the 2012 chamber experiment (Section 3.5.5.1). Again, where possible, accessions from western Asia (including the Fertile Crescent) were selected, with between one and three accessions per species.

3.5.3.2 Growth conditions

As for the 2013 glasshouse experiment (Section 3.5.2.2), prior to planting, the outer glumes of the grasses were removed (where necessary), the legumes were scarified with sand paper to break seed dormancy and the fresh seed mass of individual seeds was measured. Seeds were germinated during March 2013, in batches of 12 seeds per species in trays containing plastic inserts with a 1:1 mixture of John Innes no. 2 compost (LBS Garden Warehouse, Lancashire, UK) and Chelford 52 washed sand (Sibelco UK Ltd, Sandbach, UK). The growth medium was saturated with water and seeds were placed in rows to enable individuals to be identified throughout germination.

In-line with the experimental conditions of the previous glasshouse experiments (Sections 3.5.2.2 and 3.5.4.2) and controlled CO₂ experiments (see section 3.5.5.2, and also Cunniff, 2009, pp. 118-19), the trays were placed in two controlled environment growth chambers (Conviron BDR16, Conviron, Winnipeg, MB, Canada) with conditions set to 20/10°C (day/night), an 8 hour photoperiod and photosynthetic photon flux density (PPFD) of 300 μ mol m⁻²s⁻¹. The controlled-environment growth chambers were set at different CO₂ levels: pre-domestication 24 Pa and current ambient 38 Pa. The controlled environment (CE) chambers were operated on a closed configuration, by connecting the outlet vent to the air inlet via a filter packed with a layer of activated charcoal and a layer of soda lime (Sofnolime 1.0- to 2.5-mm granules, Molecular Products Ltd, Mill End, Essex, UK) (Cunniff et al., 2017). The activated charcoal was used to filter the air and eliminate any traces of gases such as ethylene, which could be emitted by plants or soil and have the potential to affect plant development (Cunniff et al., 2017, Cunniff et al., 2008). The CO₂ level in the chambers was controlled using a CO₂ sensor (CARBOCAP® Carbon Dioxide Probe GMP343, Vaisala, Finland) that was linked to a feedback system regulating the circulation of chamber air through the soda-lime scrubber, and $CO₂$ level was recorded every minute (Cunniff et al., 2008). The soda-lime was changed as soon as $CO₂$ level started to drift above the target level, which was approximately every four weeks (Cunniff et al., 2008).

Once the seedlings had reached the two-leaf growth stage, the plants were subject to a 10 week vernalisation period to promote flowering. The same growth chambers were used, with a constant temperature of 4° C (day and night), and the same CO₂ conditions, PPFD and photoperiod as for germination. Following vernalisation treatment, three seedlings per species were selected for each of the two $CO₂$ treatments (equating to three replicates per species, per CO₂ treatment). The seedlings were planted in 5 L tubular pots containing a 1:1 mixture of John Innes no. 2 compost and fine vermiculite (1-3 mm, Sinclair, Cheshire, UK). At this stage vermiculite substituted for sand, in order to make the growth mix lightweight and accommodate the capacity of the CE chambers in terms of weight restrictions. After vernalisation the CE chambers conditions were adjusted; temperature was returned to $20/10^{\circ}$ C (day/night) with a photoperiod of 16 hours and PPFD to a maximum level of 650 μ mol photons m⁻²s⁻¹ measured at canopy height (following Cunniff, 2009, p. 118). Vapour pressure deficit (VDP) had a minimum value of 0.2 kPa at night and a maximum value of 0.7 kPa during the day until grain filling, when it was increased to 0.5 kPa at night and 0.9 kPa during the day to facilitate maturation (following Cunniff, 2009, p. 118).

Treatments and plants were exchanged between the two growth chambers on a weekly basis, from germination to maturity, to eliminate the confounding effects of the chamber and growth

environment. In the early stages of the experiments, plants were watered three to four times a week, but again, this was reduced at grain filling and watering ceased when grain filling was complete and senescence had commenced. Plants were fertilised once during the experiment, after two months of growth, with the minimum recommended dose of Osmocote Pro slow release fertilizer added to each pot.

3.5.3.3 Experimental design and measurements

Within each environment controlled (CE) chamber for the two $CO₂$ treatments, a randomised planting design was used, consisting of 84 containers per chamber with three replicates per species where possible (including both grasses and legumes). For stability and ease of transfer between chambers, the 84 containers were arranged into 15 rows; each row comprised two sets of three containers secured together with cellotape (Figure 3.13). During the weekly chamber and treatment exchange, the rows within each treatment were also cycled for the duration of the experiment. Wooden canes were placed in each pot and garden twine used to ensure the plants retained an upright growth habit.

At maturity plant trait measurements were taken, with between one and three replicates per species (some seedlings failed to establish or remained in the vegetative growth stage). Canopy height and diameter were measured (protocols as described in section 3.3.2.1.1), and fresh leaf material was collected for fresh leaf trait measurements (including SLA, DMC, as described in Section 3.3.2.1.2), and stomatal length and density, as outlined in Section 3.3.2.2.1).

3.5.4 2012 Glasshouse experiment

As part of the Origins of Agriculture project (a collaborative project between the Department of Animal and Plant Sciences and the Department of Archaeology, University of Sheffield), a seed yield experiment was conducted in order to replicate grasses growing in stands (see 'equal seed mass experiment' in Preece et al., 2018). The author was given permission to take non-destructive trait measurements relating to the duration and quality of growth (i.e. canopy height and diameter) of the crops, crop progenitors and wild species.

3.5.4.1 Plant material

The plants grown as part of this experiment comprised 18 grass species, including domesticates *Hordeum vulgare, Triticum monococcum, T. dicoccum*, together with their wild progenitors (*H. spontaneum, T. baeoticum, T. dicoccoides*), and wild species from the Fertile Crescent that were never domesticated (Table 3.10). Two species that are later domesticates (*Avena sativa* and *Secale cereale*) were also grown, along with their progenitor species, *S.*

vavilovii (progenitor of rye), *A. sterilis* and *A. fatua* (likely progenitors of oat). The selection of other wild species was based on their presence (or the presence of the genus to which they belong) in the archaeobotanical database (Wallace et al., 2019). Seeds were provided by the National Plant Germplasm System (United States Department of Agriculture, Beltsville, MD, USA) and IPK Gaterslaben Genebank (Stadt Seeland, Germany) (Table 3.10); where possible two accessions were used per species, the accessions chosen were collected predominantly from southwest Asia, and seeds were selected to span a range of seed size within each species (Preece et al., 2018).

3.5.4.2 Growth conditions

The growth conditions (including seed preparation, germination and growth medium used) are as described in Preece et al. (2018, pp. 3-4) and are consistent with those for the 2013 glasshouse experiment (as described in section 3.5.2.2). Following germination and a 6-8 week vernalization period in controlled environment chambers (within the Sir David Read Controlled Environment Facility, University of Sheffield, UK), plants were transferred to a glasshouse (Arthur Willis Environment Centre, University of Sheffield, UK) where individuals were planted in monocultures within 11 L square pots (21 cm x 21 cm x 25 cm). The same growth mixture as for germination was used (Preece et al., 2018), in order to imitate the growth of grasses in stands. Each pot contained 0.4g seed, and thus the number of seedlings per pot varied depending on the mean seed mass of the accession; Preece et al. (2018) provide a reference for the approximate number of individuals per pot, where the largest-seeded species, *Secale vavilovii* had 11 or 14 individuals per pot (depending on the accession) and the smallestseeded species, *Eremopyrum bonaepartis*, had 181 or 266 individuals per pot. In addition, the minimum recommended dose of Osmocote Pro slow release fertilizer was added to each pot. The temperature in the glasshouse was maintained at 24° C/15°C (day/night) with a 12 hour photoperiod, and was naturally sunlit during the high-light conditions of summertime, with additional light provided on cloudy days (Preece et al., 2018).

3.5.4.3 Experimental design and measurements

Within the glasshouse a randomised block design was used consisting of six blocks in total with each block containing one pot of each species, where possible (Figure 3.14). In order to ensure plants remained in an upright growing habit, wooden canes were placed within the pots and garden twine used to help retain the plants. Three species are self-incompatible in terms of pollination (*Secale cereale*, *Secale vavilovii* and *Secale strictum*) and cross-pollination was therefore carried out manually, using a paintbrush.

At maturity, after two months of growth, plant trait measurements were taken for a focal plant (within each pot) in the subset of replicates for each species (between one and four replicates per species). The non-destructive traits measured for this research were canopy height and diameter.

3.5.5 2012 Controlled growth experiment

As part of the "Evolutionary Origins of Agriculture" project, cereal progenitors and other wild annual grasses were germinated and grown under post-glacial CO₂ levels (27 Pa) that prevailed at the beginning of the Holocene. In the process of these experiments, vernalised seedlings that were surplus to requirements were made available to the author for growth to maturity and measurement. The seedlings were grown on to maturity under current $CO₂$ conditions (~38 Pa). In addition, surplus vernalised seedlings of *Avena sterilis* (grown in glasshouse conditions, germinated and vernalised under 'high' current ambient CO₂ levels) were used in this growth chamber experiment.

3.5.5.1 Plant material

The plants available for this experiment comprise 10 grass species, including 'founder' wild progenitors *Hordeum spontaneum, Triticum aegilopoides* and *T. dicoccoides* and secondary progenitor *Avena sterilis*, and six wild grass species that occur in the Fertile Crescent but that were never domesticated (Table 3.11). As before, the selection of wild grasses was on the basis of archaeobotanical evidence from the archaeobotanical database (Wallace et al., 2019). Seeds were obtained from the National Plant Germplasm System (United States Department of Agriculture, Beltsville, MD, USA), IPK Gaterslaben Genebank (Stadt Seeland, Germany) and the Millennium Seed Bank (Kew Gardens, Wakehurst Place, UK). Where possible, accessions from southwest Asia (including the Fertile Crescent) were selected, with between three and seven accession per species (Table 3.11).

3.5.5.2 Growth conditions

The seeds were prepared by removal of outer glumes and fresh individual seed mass measured. The seeds for the controlled environment experiment were germinated in compartmentalised petri dishes (Sterilin™ 100mm square petri dishes) on filter paper saturated with water, enabling germination to be tracked for individuals. For the germination of *Avena sterilis* seeds, see Section 3.5.2.2. The trays were placed in three controlled environment (CE) chambers (Conviron BDR16, Conviron, Winnipeg, MB, Canada) per CO₂ treatment, located within the Sir David Read Controlled Environment Facility, University of Sheffield, UK. The operation of the controlled environment (CE) chamber and control

measures employed to filter the chamber air and maintain CO₂ at the target levels (i.e. the use activated charcoal and replenishment of soda-lime) are as described in Section 3.5.3.2.

Temperature in the growth chamber was set to 20/15°C (day/night), with a 12 hour photoperiod and a relative humidity of 70% (Osborne, C. 2018, *pers. comm*.)*.* Following germination, individual seedlings were transferred to 0.1 L compartments of planting trays containing 1:1 vermiculite: Levington M3 compost (ICP, Ipswich, Suffolk, UK). The plants were watered three to four times a week. When the three-four leaves were produced, the seedlings were subject to a ten week vernalisation treatment to stimulate flowering, with a constant temperature of 4°C (day and night) (Osborne, C. 2018, *pers. comm*.) and the same PPFD, photoperiod and $pCO₂$ conditions as during germination. Treatment and plants were exchanged between the three growth chambers on a weekly basis from germination to harvesting, to eliminate the confounding effects of the chamber and growth environment (Osborne, C. 2018, *pers. comm*.).

Following the vernalisation treatment, plants surplus to the EOA controlled environment experiment and the additional *Avena sterilis* plants were transferred to a growth room (MTPS 120, Conviron, Winnipeg, MB, Canada). The CO₂ in the growth room was modern ambient (\sim 38 Pa), the temperature was set to 24/20 °C (day/night) with a 14 hour photoperiod, stepping up to a maximum light intensity over 4 hours, and down again over 2 hours and constant 60% relative humidity (Kluyver et al., 2013, p. 104). Maximum light intensity at canopy height was around 1200 μ mol m⁻²s⁻¹ (Kluyver et al., 2013, p. 104). Individual seedlings were planted in 1.5 L square pots (13 cm x 13 cm x 13 cm), with the same growth medium as used for vernalisation.

3.5.5.3 Experimental design and measurements

Between two and seven replicates per species were grown on for measurement, with additional plants grown to maturity for the purpose of generating seed for further experiments. Within the growth room, a randomised block design was used consisting of three blocks with between 45 and 49 individuals (depending on plant mortality) (Figure 3.15). The use of the high nutrient Levington M3 compost negated the need for application of additional fertilizer during the growth period. The pots were placed in trays and bottom-watered three to four times a week; the frequency of watering was reduced at grain filling and terminated once grain filling was complete and senescence had commenced.

After two months of growth, at maturity, plant trait measurements were taken from 45 individuals, one per accession per species (where available), equating to between two and

seven replicates per species. The 'whole plant' traits measured for this research comprised canopy height and diameter (protocols as described in Sections 3.3.2.1 and 3.3.2.2). Fresh leaf material was collected for the leaf trait measurements, SLA and DMC, as described in section 3.3.2.1.2).

3.6 Data preparation and manipulation

3.6.1 Preparation of database

Trait data for individual experimental plants and field collections (including those abstracted from the functional ecological databases) were compiled into a single database, with data for the following eight attributes: DMC, SLA, leaf area:thickness, stomatal density, stomatal length, canopy height, canopy diameter and genome size class. From this dataset, species attribute means were calculated for the field collections, first by geographic region (i.e. Near East, southern Europe and northern Europe) and then by species alone (i.e. combined species means for all regions). For the growth experiments, species attribute means were calculated per experiment (and separate treatment – high or low $CO₂$ levels for the 2013 growth chamber experiment).

In order to explore the data, individual plants, field collections or species were coded by family, geographic region or experimental source, domestication status, CO₂ level and genome size class.

3.6.2 Principal components analysis

A 'data reduction' technique, principal components analysis (PCA), was used in order to summarise the underlying patterns of correlation (Pallant, 2016, p. 108). This technique was chosen as PCA attempts to produce a smaller number of linear combinations of the original variables, in a way that accounts for most of the variability in the patterns of correlations (see Pallant, 2016, Chapter 15). PCA was performed using IBM SPSS (version 24) and the rotational approach adopted was an orthogonal (uncorrelated) Varimax method, which attempts to minimise the number of variables that have high loadings on each component (Pallant, 2016, p. 186). The number of principal components to retain for each PCA was considered in relation to the eigenvalues where, for the majority of the analyses, only factors with an eigenvalue of 1.0 or more were retained for further investigation. A small number of the PCA analyses produced one component using this criterion and, in these circumstances, reducing the eigenvalue to 0.9 was sufficient to extract two components. In order to confirm the number of components to retain, Cattell's (1966) scree test and Horn's (1965) parallel analysis, the latter

using software program Monte Carlo PCA for parallel analysis (Watkins, 2000), were also performed for each analysis (with >100 cases).

The principal components analyses (PCA) were conducted in successive stages. The first stage was to establish whether principal component axes were robust regardless of taxonomic family (grasses versus legumes), methodological source (field collections or experimental plants), or data source (geographic region or individual experiment). PCA was therefore performed on the entire dataset, then on data reduced to grasses only or legumes only, and on data reduced to field collections or experimental plants. These PCAs were based first on attribute values for individual collections/plants, and then on species attribute means. The results of the earlier analyses were used to determine the level of amalgamation appropriate for the calculation of species means in subsequent analyses.

The aim of the second stage of analysis was to determine whether there were trait differences between domesticated species, wild progenitor species and other wild species that were never domesticated. Again, the structure of these analyses was informed by the results of the earlier analyses.

Chapter 4: Results

4.1 Introduction

This chapter examines the ecological traits of domesticated crops, their wild progenitors, and other wild species that were never domesticated, by presenting the results of analyses of functional ecological data from growth experiments and field collections. The functional attributes included in the analyses, with their ecological significance, are given in Table 3.1. The attributes available for each growth experiment differ, however: for the 2012 glasshouse experiment only canopy data are available, for the 2012 growth chamber experiment stomatal data are unavailable, and for the 2013 glasshouse experiment canopy data are absent.

To maximise the amount of data that can be included in the analyses as a whole, therefore, three combinations of plant functional attributes were used in principal components analyses (PCAs) to explore functional variation: (1) all seven attributes, including the three leaf attributes (leaf dry matter content (DMC), specific leaf area (SLA) and leaf area:thickness), the two stomatal attributes (stomatal length and density) and the two canopy attributes (height and diameter); (2) the three leaf attributes and the two stomatal attributes; and (3) the three leaf attributes and two canopy attributes. Analyses (2) and (3) include fewer attributes but allow a larger number of experimental plants to be included in the analyses.

In plots of principal components analyses, each axis is labelled, where possible, according to its primary ecological significance: axes dominated by SLA and DMC relate primarily to the ability to respond to fertile conditions, canopy attributes primarily to the ability to respond to fertility in the absence of disturbance, and stomatal attributes primarily to water-use efficiency, and so are labelled, respectively, 'fertility', 'fertility (minus disturbance)' and 'water'. For the sake of brevity, these labels are also used in the text to refer to these axes of variation.

4.2 Preliminary analyses

Before comparing the functional characteristics of domesticated, progenitor and wild species, three other factors that might potentially contribute to differences in the functional attributes of individual plants or species were considered: (1) family (grasses or legumes); (2) geographic location of field collections; (3) inadvertent differences in experimental conditions.

4.2.1 Comparison of families

4.2.1.1 Differences related to taxonomy

In order to compare the functional characteristics of grasses and legumes, a principal components analysis was conducted on all seven functional attributes of all the individual field collections and experimental plants (including both grasses and legumes, wild and domesticated) for which values of all seven attributes were available. The first three principal components extracted by the analysis reflect the three main ecological characteristics measured by these attributes: water-use efficiency (axis 1, with stomatal length loading negatively (to the left in Figure 4.1a) and stomatal density positively (to the right)), the ability to respond to fertility in the absence of disturbance (axis 2, canopy height and diameter loading positively (towards the top in Figure 4.1a)), and the ability to respond to fertile conditions (axis 3, SLA loading positively and DMC negatively (not shown)). The points representing individual plants were coded (in Figure 4.1b) according to the family to which they belong, which shows that there is a strong tendency for legumes to be characterised by larger numbers of smaller stomata compared to grasses which tend to have fewer, larger stomata (Figure 4.1b, axis 1). There is no distinction between grasses and legumes along either fertility axis (see, for example, Figure 4.1b, axis 2).

To see whether this difference in water-use efficiency is apparent for both the field collections and the experimental plants, separate analyses were carried out on each group. Because the overall distinction between grasses and legumes is that of water-use efficiency, rather than fertility, these analyses were conducted on leaf and stomatal attributes only, which has the advantage that the data from the 2013 glasshouse experiment (which lacked canopy measurements) could also be included in the analyses.

In the analysis using the field collections, the first component reflects water-use efficiency (stomatal number and length, though loading in the opposite direction to the previous analysis) and the second the ability to respond to fertile conditions (SLA and DMC) (Figure 4.2a). There is again a strong tendency for legumes to be characterised by larger numbers of smaller stomata compared to grasses (Figure 4.2b). In the analysis using the experimental plants, the first and second components again reflect water use efficiency and the ability to respond to fertile conditions respectively (SLA and DMC loading in opposite directions on the second axis) (Figure 4.3a). There is a slight tendency for legumes to be characterised by larger numbers of smaller stomata compared to grasses (Figure 4.3b).

To determine whether the difference in water-use efficiency between grasses and legumes is apparent when mean attribute values (calculated by geographic region for the field collections and by individual experiment for the experimental plants) for each species were used, separate analyses, using the leaf and stomatal attributes, were performed for the field collections and the experimental plants. As for the analyses using individual field collections and experimental plants, the first two components in the analyses using attribute means reflect water-use efficiency (stomatal number and length), and ability to respond to fertile conditions (SLA and DMC) respectively (Figures 4.4a and 4.5a). In both cases the difference in water-use efficiency between grasses and legumes is, if anything, slightly stronger when using species attribute means than it was when individual plants were used (Figures 4.4b and 4.5b).

4.2.1.2 Differences related to genome size

Stomatal size was estimated by measuring the length of one of the guard cells, and research has demonstrated that cell size (and consequently stomatal length) is correlated with genome size (e.g. Beaulieu et al., 2008, Knight and Beaulieu, 2008, Hodgson et al., 2010, Jordan et al., 2015). So, to determine whether the overall difference in stomatal length between grass and legume species might be attributable to a difference in genome size between the two families, a principal components analysis was conducted using leaf and stomatal attributes, and species means for all the field collections and experimental plants for which these attributes were measured. The first two components extracted by the analysis again reflect the ability to respond to fertile conditions (this time along axis 1, SLA loading positively and DMC negatively) and water-use efficiency (axis 2, stomatal number loading negatively and length positively) (Figure 4.6a). The species points in plots of axes 1 and 2 were coded first by family (Figure 4.6b) and then by genome size (Figure 4.6c), indicating that there is a functional difference relating to both taxonomic family and genome size (which are themselves highly correlated).

4.2.1.3 Outcome

Broadly speaking, there are differences in water-use efficiency between the grass and legume species used in this study, which is in line with previous research on stomatal traits that include comparisons of species from these two families (Beaulieu et al., 2008, p. 981). Comparing Figures 4.6b and 4.6c, it is difficult to determine whether genome size or taxonomic affiliation to family is primarily responsible for this functional difference: the species with the very smallest stomata are concentrated towards the 'drier' (lower) end of axis 2, as would be expected (Hetherington and Woodward, 2003, Beaulieu et al., 2008, p. 984, Hodgson et al., 2010) and this includes a few grass species; on the other hand, a few legume species with larger genomes are also located towards this end of the axis despite their larger genome size. It is possible, therefore that both genome size and taxonomic affiliation *per se* play a part in this functional difference.

Whatever the reason, given the functional difference identified between grasses and legumes, it was necessary to investigate species from these two families separately in further analyses aimed at understanding functional differences relating to domestication status.

4.2.2 Comparison of field collections and experiments

To determine whether the functional attribute data for plants collected in the field (or in botanical gardens) could be directly compared with data from the ecological experiments, principal components analyses were performed on individual plants, and the plant data points coded according to whether they are field collections, collections from botanical gardens or experimental plants.

4.2.2.1 Grasses

To maximise the number of plants included in the principal components analyses, analyses were performed using firstly the leaf and stomatal attributes and secondly the leaf and canopy attributes. The first analysis enabled the 2013 glasshouse experiment (which lacked canopy measurements) to be included, while the second analysis allowed the inclusion of the 2012 growth chamber experiment (which lacked stomatal data) and all the plants from the 2013 growth chamber experiment (some of which lacked stomatal data).

In the first analysis, as in previous analyses using the leaf and stomatal attributes, the two main components extracted reflect two ecological axes, 'water' (axis 1) and 'fertility' (axis 2) (Figure 4.7a). There is clear differentiation in relation to fertility attributes along axis 2, with the experimental plants (towards the positive (top) end of the axis), having higher SLA and lower DMC than the majority of field collections, including those from botanical gardens (Figure 4.7b). The collections from botanical gardens are concentrated towards the positive (right) end of axis 1 along with the majority of field collections, and also have similar SLA and DMC values to the field collections (Figure 4.7b, axis 2).

In the second analysis, using the leaf and canopy attributes, the first two components, as before, reflect the ecological axes 'fertility (minus disturbance)' (axis 1) and 'fertility' (axis 2) (Figure 4.8a). There was a clear tendency, as in the previous analysis, for the majority of experimental plants to plot positively on (towards the top of) axis 2, having higher SLA and lower DMC than the field collections (Figure 4.8b), though some of the experimental plants (possibly those excluded from the previous analysis due to the absence of stomatal data) plotted more negatively on this axis. There was little differentiation between the experimental plants and field collections along the first axis, though a few of the field collections have larger canopy dimensions (Figure 4.8b).

4.2.2.2 Legumes

The same two principal components analyses (described in section 4.2.2.1) were repeated for legumes. The 2012 growth chamber experiment and collections from botanical gardens are not represented in these analyses as they did not include data for legumes. The first analysis used the leaf and stomatal attributes which allows the 2013 glasshouse experiment (which lacks canopy measurements) to be compared with the field collections. As for the grasses, the first two components extracted in this analysis reflect the two ecological axes: 'water' (axis 1) and 'fertility' (axis 2) (Figure 4.9a). Legumes from the 2013 growth experiment are clearly differentiated from the field collections along the 'fertility' axis, with the experimental plants plotting towards the positive (top) end of axis 2, having high SLA and low DMC, whilst the field collections plot more negatively (towards the bottom of the axis) (Figure 4.9b). No differentiation between the experimental plants and field collections was evident along the 'water' axis (axis 1).

The second analysis, using the leaf and canopy attributes, allowed all of the 2013 growth chamber experimental plants (some of which lack stomatal data) to be compared with the field collections. As for the grasses, the first two components reflect the two ecological axes: 'fertility (minus disturbance)' (axis 1) and 'fertility' (axis 2) (Figure 4.10a). Legumes from the 2013 growth experiment are again differentiated (though slightly less clearly) from the field collections along the 'fertility' axis, the former located towards the positive (top) end of axis 2, tending to having higher SLA and lower DMC than the field collections (Figure 4.10b). The experimental plants have canopy dimensions in the same range as the majority of field collections (plotting towards the negative (left) end of axis 1, the 'fertility minus disturbance' axis) (Figure 4.10b), though a few of the field collections have larger canopies.

4.2.2.3 Outcome

The key difference between the field (including the botanical garden) collections and the experimental plants was the higher SLA and lower DMC of the experimental plants. In describing phenotypic differences between laboratory and field grown plants, Poorter et al. (2016) note that a common difference between experimental and field observations is a higher SLA for lab-grown plants. The differences in SLA and DMC may be due to better soil nutrient conditions in the growth experiments than in the natural habitats and botanical gardens, despite attempts to replicate unimproved soils for the growth experiments (see Methods, section 3.5). Plasticity in traits for morphological features that optimize light capture can also be high (Valladares and Niinemets, 2008), and it is well known that SLA responds strongly to variation in environmental conditions, increasing in response both to increased fertility and to decreasing light levels (Shipley and Almeida-Cortez, 2003, Hodgson et al., 2011). Attention has

also been drawn to the fact that light levels under experimental conditions (within glasshouses and particularly growth chambers) are often lower than those in natural conditions (Poorter and van der Werf, 1998, Shipley, 2006). The main differences between the field collections and the majority of the experimental plants, therefore, may be related more to individual plant responses to light and/or nutrient levels than a predisposition of some species to exploit fertile conditions.

These principal components analyses demonstrate that there are significant differences between the experimental plants and the field collections in relation to SLA and DMC. In light of these results, amalgamation of the attribute data from the experiments and field collections would not be appropriate, and so they were analysed separately in further analyses exploring functional differences relating to domestication status.

4.2.3 Comparison between the geographic regions of the field collections

To ascertain whether the selected functional attributes of the field collections are sensitive to geographic variation, principal components analyses were performed first on individual collections and then using species mean attribute values (averaged by geographical region). The data points representing collections were coded according to whether they are from northern Europe, southern Europe or the Near East. In addition, two groups of collections grown on from seed collected in the Near East or Europe (a) at botanical gardens (in France and Germany) and (b) in various locations in the UK, were coded separately. Separate comparisons were made for grasses and legumes, as follows.

4.2.3.1 Grasses

In the first analysis of grasses, using all seven attributes, three main components were extracted reflecting the ecological axes 'fertility (in the absence of disturbance)' (axis 1), 'water-use efficiency' (axis 2) and 'fertility' (axis 3) (Figure 4.11a, axes 2x3). There is little difference between the groups along axis 1, 'fertility (in the absence of disturbance)' (not shown). In a plot of axis 2 against axis 3 (Figure 4.11b), the grown-on plants plot negatively (towards the left) on axis 2 ('water') with the majority of the Near East collections, having fewer larger stomata, while field collections from Europe are more widely distributed, with some of the collections from southern Europe plotting more positively (towards the right). On axis 3 ('fertility'), the grown-on plants tend to plot negatively (towards the bottom) with the European collections, while some of the Near East collections plot more positively (towards the top of the axis), having lower SLA and higher DMC than the other collections (Figure 4.11b).

Separate analyses were also carried out using (1) the five leaf and stomatal attributes and (2) the five leaf and canopy attributes, with the same coding of plant data points as before. In the first of these analyses, the first two components reflect the ecological axes 'water-use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.12a). On both axes, the distribution of the collections (Figure 4.12b) is comparable to the previous analysis using all seven attributes, although the tendency for the grown-on collections (and the majority of the Near East collections) to plot negatively (towards the 'wetter', left end) of the 'water' axis is slightly weaker. In the second analysis, using the five leaf and canopy attributes, the first two components extracted reflect the ecological axes 'fertility (in the absence of disturbance)' (axis 1) and 'fertility' (axis 2) (Figure 4.13a). There is a slight tendency for the European collections (whether collected in the wild or grown-on) to plot more positively (towards the 'fertile' end) on both axes (top right) than the Near Eastern collections (Figure 13b).

Finally, analyses were performed using species mean attribute values (averaged by geographical region), again using (1) the leaf and stomatal attributes and (2) the leaf and canopy attributes (with the same coding of plant data points). The grown-on collections were not included in these means, as their seeds were often collected in one geographic region but grown on in another. The main components extracted from the first analysis reflect the ecological axes 'water use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.14a). On axis 1, there is little regional variation relating to water (Figure 4.14 b) compared to the corresponding analysis using individual collections. There is some evidence of regional variation in relation to fertility on axis 2, with northern European collections being restricted to the 'fertile' (top) end (Figure 14b). This trend is more apparent in the second analysis using the leaf and canopy attributes, where the extracted components reflect the ecological axes 'fertility (in the absence of disturbance)' (axis 1) and 'fertility' (axis 2) (Figure 4.15a). Northern European collections are located towards the positive 'fertile' end of both axes (top right, Figure 4.15b), Near Eastern collections towards the negative 'infertile' end of both axes (bottom left), with southern European collections widely dispersed across the plot.

To determine whether the differences in attribute values between different geographic regions are significant, a series of one-tailed paired t-tests were performed, using species attribute means for grass collections from the Near East, southern Europe and Northern Europe (Table 4.1). There are significant differences between the southern Europe and the Near East collections (at $p = 0.05$), with those from the Near East having significantly smaller canopy diameters, as well as lower SLA and higher DMC than those from southern Europe, as might be expected. Collections from southern Europe also have significantly fewer stomata

than those from northern Europe (at *p*=<.05) but this is the opposite of expectations and there is no significant difference in stomatal size (Table 4.1).

4.2.3.2 Legumes

The series of principal components analyses applied to grass species to identify regional variation were repeated for legume species, but no regional variation was apparent (see for example Figure 4.16 using leaf and stomatal attributes and Figure 4.17 using leaf and canopy attributes, both using individual collections and regional species attribute means).

As for the grasses, a series of one-tailed paired t-tests were performed for the species attribute means for the legume collections from the Near East, southern Europe and northern Europe (Table 4.2). There are significant differences (at *p*=<.05) in SLA and leaf area:thickness between the different geographic regions but, as often as not, these are in the opposite direction to those that might be expected, notably for leaf area:thickness (Table 4.2).

4.2.3.3 Outcome

Overall, there is evidence for some regional variation in functional attributes relating to environmental conditions for the grasses (though not for the legumes), with the collections from the Near East tending to have smaller canopies, lower SLA and higher DMC than the European collections. This variation is of a similar magnitude to that found in previous analyses of the full dataset of field collections (Jones et al., 2005: Table 3), where it was demonstrated that functional attribute data from one region could be successfully used to characterise species' environmental preferences in another region.

To test whether the regional differences in some attributes were great enough to influence the final interpretations of the data in terms of domestication status, mean species attribute values were re-calculated using the combined measurements from all three geographic regions, and the analyses repeated. The plots based on these overall mean values were then compared with the plots using the mean values calculated separately for each region, with both sets of plots coded by domestication status. Despite the observed regional variation in canopy size, SLA, and DMC, the positioning of domesticated species, their wild progenitors and other wild species points was very similar in both sets of plots. The results presented in the rest of the chapter are therefore based on the mean values from field collections in all three geographic regions, to maximise the sample size used in the calculation of species means for the measured attributes.
4.2.4 Comparisons of experiments

To ascertain whether the functional attributes of the experimental plants were sensitive to experimental conditions other than the domestication status of the species, principal components analyses were performed, with the data points representing individual plants or species means coded according to experimental source (Figures 4.18-4.21). These results were used to compare the functional attributes of first plants from different experiments and secondly plants grown under the two carbon dioxide ($CO₂$) treatments in the 2013 growth chamber experiment: current (38 Pa) CO₂ levels and late Epipalaeolithic (24 Pa) CO₂ levels. Separate comparisons were made for grasses and legumes, as follows.

4.2.4.1 Grasses: Comparison between experiments

The first analyses of grasses used the five leaf and stomatal attributes, which enables a comparison between the 2013 growth chamber and 2013 glasshouse experiments (the latter of which lacks canopy data). In the analysis using individual plants, the first two components extracted reflect ecological axes 'water-use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.18a). There is strong differentiation between plants from the 2013 growth chamber (both treatments) and the 2013 glasshouse experiments on axis 1 (water) (Figure 4.18b). The glasshouse plants plot more positively (to the right) on this axis, tending to have fewer larger stomata than the growth chamber plants, most of which plot towards the negative end (left) of the axis. On axis 2 (fertility), a few plants from the 2013 glasshouse experiment plot towards the negative (bottom) end of the axis (Figure 4.18b), having high SLA and low DMC compared to the majority of plants. In the analysis using species means, the first two components extracted again reflect ecological axes 'water-use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.19a). The differentiation of the 2013 glasshouse and 2013 growth chamber experiments is more apparent on both axes (Figure 4.19b).

A second set of analyses used the five leaf and canopy attributes enables a comparison between the 2012 and 2013 growth chamber experiments (the former of which does not include stomatal data). In the analysis using individual plants, the first two components extracted reflect ecological axes 'fertility' (axis 1) and 'fertility (in the absence of disturbance)' (axis 2) (Figure 4.20a). On axis 1 ('fertility') there is a very clear separation of the two experiments (Figure 4.20b), with the 2013 growth chamber plants plotting towards the negative end (left) of the axis, having markedly higher SLA and lower DMC than the 2012 growth chamber plants, the latter which plot towards the positive (right) end of the axis. On axis 2 (fertility, in the absence of disturbance), the majority of plants from both experiments

plot within the same range (Figure 4.20b), having similar ranges of canopy dimensions and leaf area:thickness ratios.

In the analysis using species means, the data available for comparison were maximised by substituting the 2013 glasshouse results (where canopy data was lacking) with canopy height and diameter measurements from the 2012 glasshouse experiment, when the same species were grown in both experiments. This enables a three-way comparison between the combined (2012/2013) glasshouse experiments, the 2012 growth chamber experiment and the 2013 growth chamber experiment. The first component extracted by this analysis primarily reflects the ecological axis 'fertility', as before with SLA loading negatively (to the left) and DMC positively (to the right). On the second axis, however, while canopy height loads positively, canopy diameter is in a relatively neutral position (Figure 4.21a). This is almost certainly due to the fact that the substituted canopy dimensions from the 2012 glasshouse experiment were derived from plants grown several to a pot rather than individually as in the other experiments, thus impeding their ability to spread laterally. There is a very clear separation of the different experiments on axis 1 ('fertility'). The species from the glasshouse experiments plot towards the negative (left) of the axis (having high SLA and low DMC compared to most of the species from the growth chamber experiments), whilst the species from the 2012 growth chamber experiment plot towards the positive (right) end of the same axis (having lower SLA and higher DMC than species from the other experiments). The species from the 2013 growth chamber experiment are located in a relatively neutral position on this axis (Figure 4.21b). On axis 2, the majority of the species from each experiment plot within similar ranges in terms of (primarily) canopy height, though a few species grown in the 2012 glasshouse and 2012 growth chamber experiments have taller canopies than the species grown in the 2013 growth chamber experiment (Figure 4.21b).

When the plot is coded by species, however, it is apparent that the six species occurring in all of the experiments (including both 'low' and 'high' CO₂ treatments in the 2013 growth chamber experiment) are positioned similarly with respect to axis 2 (Figure 4.22b). This indicates that phenotypic trait variation within species (intraspecific variability) is negligible in terms of (primarily) canopy height, and that in relation to this trait, comparisons between species (i.e. interspecific variability) are consistent for each experiment.

4.2.4.2 Grasses: Comparison of CO₂ treatments within the 2013 growth chamber experiment

In analyses using the leaf and stomatal attributes, for both individual plants and species means), no differentiation between the plants grown under the two $CO₂$ treatments is

apparent on either axis (Figures 4.18b and 4.19b). Similarly, in analyses using the leaf and canopy attributes, there is again no differentiation on either axis between the two $CO₂$ treatments (Figures 4.20b and 4.21b). A series of paired t-tests was also performed, using species mean attribute values, to determine whether any significant functional differences between the two treatments could be detected. Only two attributes (canopy height and diameter) are significantly greater (at $p = <.05$) at higher CO₂ levels, whilst SLA which also relates to productivity, is significantly lower (Table 4.3).

4.2.4.3 Legumes: Comparison between experiments

Since there were no legume species in the 2012 growth chamber or 2012 glasshouse experiments, comparisons could only be made between the 2013 glasshouse and 2013 growth chamber experiments. Comparisons were made using leaf and stomatal attributes, as canopy dimensions were not available for the former. The first two components extracted by both analyses reflect ecological axes 'fertility' (axis 1) and 'water use efficiency' (axis 2) (Figures 4.23a and 4.24a). No functional differences between the glasshouse and growth chamber experiments were apparent on any axis, either for the analysis using individual plants (Figure 4.23b) or for the analysis using species means (Figure 4.24b).

4.2.4.4 Legumes: Comparison of CO₂ treatments within the 2013 growth chamber experiment

In analyses using the leaf and stomatal attributes, for both individual plants and species attribute means, no differentiation between the plants grown under the two $CO₂$ treatments is apparent on either axis (Figures 4.23b and 4.24b). In the analyses using the five leaf and canopy attributes, for both individual plants and species attribute means, the first component extracted reflects the ecological axis 'fertility' (SLA/DMC) whilst the second component primarily reflects canopy height (canopy diameter plots more neutrally) (Figures 4.25a and 4.26a). The two $CO₂$ treatments are not distinguishable on either axis for either individual cases (Figure 4.25b) or species means (Figure 4.26b). To determine whether any significant functional differences could be detected between species grown under the 'high' and 'low' $CO₂$ treatments, a series of paired t-tests was performed, using species mean attribute values. Stomatal density, which relates (positively) to water use efficiency, is significantly higher (at p=<.05) at higher CO₂ levels (Table 4.4), as is DMC, which relates (negatively) to productivity.

4.2.4.5 Outcome

In the comparison between the experiments on grass species, two main differences were identified. Firstly, the plants grown in the 2013 growth chamber possess functional attributes (smaller, more numerous stomata) indicating greater water use efficiency than those grown in

the 2013 glasshouse experiment. This is unlikely to reflect different watering regimes, as both experiments were subjected to a similar regime. Other differences in environmental conditions (e.g. day length, night/day temperatures or light intensity) may have affected transpiration rates (Witkowski and Lamont, 1991, Shipley and Almeida-Cortez, 2003, Poorter et al., 2016) and so account for this difference in stomatal attributes. Secondly, the different experiments were clearly distinguished by attributes relating to fertility (SLA and DMC). This again may relate more to individual plant responses to different growing conditions between experiments (in this case, light or nutrient levels) than to a predisposition of some species to exploit fertile conditions (as suggested to explain differences in fertility attributes between field collections and experimental plants (Section 4.1.2.3)). Given the differences in plant functional attributes between experiments, due to unintended variation in experimental conditions, species means were calculated separately for each experiment.

Regarding responses to the high (current) and low (Late Epipalaeolithic) $CO₂$ treatments, there are no apparent differences in relation to any of the ecological axes extracted in the principal components analyses for either grasses or legumes, and the results of the paired t-tests are inconsistent. While small but significant differences were detected for canopy height and diameter for the grasses, indicating that the plants grown at higher $CO₂$ had slightly larger canopies (as might be expected (Cunniff et al., 2008, 2016, Cunniff, 2009)), SLA, which also indicates greater productivity, is significantly lower (which is the opposite of expectations). For legumes, stomatal density is significantly higher at high CO₂ levels but there was no correspondingly significant decrease in stomatal size, which would indicate water-use efficiency (as might be expected at higher CO₂ levels (Cunniff et al., 2008, 2016)), whilst DMC, which relates (negatively) to productivity is significantly higher (the opposite of expectations). The potential effects of $CO₂$ levels on species of different domestication status will be considered in Section 4.3.

4.3 Functional differences in relation to domestication status

Having taken account of geographic and experimental variation in functional attributes, it is now possible to consider the effects of domestication status on plant functional attributes. It will also be possible to determine whether observations made concerning domestication status on plants that grew under current atmospheric CO₂ levels are applicable to plants that grew under the CO₂ conditions that prevailed at the time of early (pre-domestication) cultivation.

4.3.1 Field collections

In this section, the principal components analyses are based on the combined mean species attributes of all geographic areas (see section 4.2.3.3 above). Separate principal components analyses were performed on grasses and legumes, in order to determine what the functional differences are between domesticated species, their wild progenitors and other wild species. Analyses were carried out first using the five leaf and stomatal attributes, and then the five leaf and canopy attributes, with species data points coded according to domestication status (domesticated, progenitor or other wild species).

4.3.1.1 Grasses

The first two components extracted in the analysis using the five leaf and stomatal attributes reflect ecological axes 'water-use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.27a). On axis 1, there is a strong tendency for the three domesticated species (*Hordeum vulgare* subsp*. distichum*, *Triticum dicoccum* and *T. monococcum*) and their wild progenitors (*H. spontaneum*, *T. dicoccoides* and *T. monococcum* subsp. *aegilopoides*) to plot towards the negative (left, 'wetter') end of the axis, having fewer larger stomata than the majority of other wild grasses (Figure 4.27b). On axis 2, the domesticated and progenitor species plot more or less neutrally (Figure 4.27b) but, in each case, the domesticated species plots more positively (towards the top, more fertile end) than their corresponding progenitors, having higher SLA and lower DMC (Figure 4.27c).

To determine whether the tendency for domesticated and progenitor species to have larger stomata than many of the other wild grasses is linked to larger genome size (as it was for grasses compared to legumes – Section 4.1.1), the same plot was coded by genome size class. There is a clear distinction along axis 1, with species having very small genome sizes (IC-values <1.4 pg) plotting positively (towards the right, drier end) (Figure 4.27d), whilst species with the largest (intermediate) genome sizes (IC-values 3.5-14 pg) plot negatively (towards the left, wetter end). Species with small genomes (IC-values 1.4-3.5 pg) plot with those of intermediate genome size or slightly more neutrally. The domesticated wheat species and all three progenitor species are part of the cluster of species in the largest (intermediate) genome size class. No genome size value was available for *Hordeum distichon* (two-row domesticated barley) but *H. vulgare* (six-row domesticated barley) also belongs to the same genome size class as the other primary domesticates (Bennett and Leitch, 2012).

In the analysis using the five leaf and canopy attributes, the first two components extracted reflect ecological axes 'fertility (in the absence of disturbance)' (axis 1) and 'fertility' (axis 2)

(Figure 4.28a). On axis 1, the domesticated and progenitor species plot towards the positive (right, more fertile) end of the axis (Figure 4.28b) and, for barley and emmer wheat, the domesticated species plot more positively than their progenitors (einkorn wheat and its progenitor plotting together on this axis). On axis 2, domesticated species and their progenitors plot more or less neutrally, and again, each domesticated species plots more positively than its progenitor.

While the principal focus of this research is to explore the functional attributes of the primary domesticates (founder crops) and their wild progenitors, data for one non-founder domesticated species (*Triticum timopheevii*) and the likely progenitors of two secondary domesticates (*Avena sterilis*, *A. fatua and Secale vavilovii*) as well as the putative progenitors of one potentially 'lost' crop (*Triticum urartu*), were included in both of the analyses described above. The axes extracted by these analyses are very similar to those excluding these 'nonfounder' species (Figures 4.29a and 4.30a), except that leaf area:thickness plays a greater role on axis 2 in Figure 4.29a, loading in the same direction as SLA. In both analyses, the nonfounder domesticated species and progenitors plot with the primary domesticates and their progenitors (Figures 4.29b and 4.30b), and this group as a whole plots more positively (towards the top, fertile end) on axis 2 in Figure 4.29b than before. In addition, these secondary or 'lost' domesticated and progenitor species also fall into the larger (large or intermediate) genome size classes.

4.3.1.2 Legumes

As for the grasses, in the analysis using the five leaf and stomatal attributes, the first two components extracted reflect ecological axes 'water-use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.31a). Only one legume progenitor species is represented (*Pisum elatius*) in this analysis, and this plots towards the negative (left, wetter) end of axis 1, having fewer larger stomata than the majority of the other wild legumes, and towards the positive (top, more fertile) end of axis 2, having higher SLA and lower DMC than most of the other wild legumes (Figure 4.31b). To determine whether the larger stomatal length of the *Pisum* progenitor is linked to larger genome size, as was the case for the cereal progenitor species (and domesticates), the same plot was coded by genome size class (Figure 4.31d). There is again a clear distinction along axis 1, with species having very small genome sizes plotting positively (towards the right, drier end) (Figure 4.31d), whilst species with small or intermediate genome sizes plot negatively (towards the left, wetter end), which as anticipated includes the *Pisum* progenitor.

In an analysis using the five leaf and canopy attributes, the first two components extracted reflect (as for the grasses) ecological axes 'fertility (in the absence of disturbance)' (axis 1) and 'fertility' (axis 2) (Figure 4.32a). Two domesticated species (*Pisum sativum* and *Lens culinaris*) and one progenitor (*Pisum elatius*) are included in this analysis. Domesticated *Pisum* and its wild progenitor plot in the top right quadrant towards the positive (more fertile) ends of both axes (Figure 4.32b), tending to have larger canopy dimensions, higher SLA and lower DMC than the majority of other species. However, domesticated *Lens* plots towards to the negative (left) end of axis 1, having smaller canopy dimensions than the *Pisum* species, and neutrally on axis 2 (Figure 4.32b).

The implications of these results for understanding the domestication process and the origins of agriculture will be discussed, along with the experimental results in the next chapter.

4.3.2 Experiments

As for the field collections, the species plots from the principal components analyses performed on the experimental plants (sections 4.2.4), using mean attribute values, were recoded according to domestication status in order to determine whether there are functional differences between domesticated species, their wild progenitors and other wild species. In addition, to investigate whether the attributes of plants of different domestication status were differentially affected at different CO₂ levels, plants grown under current and late Epipalaeolithic CO₂ levels in the 2013 growth chamber experiment were coded separately. The recoded plots, using the five leaf and stomatal attributes, and the five leaf and canopy attributes are presented first for grasses and then for legumes.

4.3.2.1 Grasses

The species plot resulting from an analysis of the five leaf and stomatal attributes for grasses (Figure 4.19b) was recoded by domestication status (Figure 4.33b). This analysis incorporates the 2013 glasshouse and 2013 growth chamber experiments, for which both leaf and stomatal attributes are available. The first two components extracted reflect ecological axes 'water-use efficiency' (axis 1) and 'fertility' (axis 2) (Figure 4.33a). On axis 1, the progenitor species tend to plot towards the positive (right, wetter) side of each experimental cluster (Figure 4.33b), the progenitors tending to have fewer, larger stomata than the other wild species in the experiment, which is in line with the field collections. This also applies to plants grown under both CO₂ treatments in the 2013 growth chamber experiment. As with the field collections, there is no apparent distinction on axis 2 (fertility) between the progenitor species and other wild species, for either experiment or CO₂ treatment (Figure 4.33b). Within each experiment, however, there is a tendency for *Hordeum spontaneum* to plot more positively on axis 2

(fertility), having relatively higher SLA and lower DMC than the other progenitors (*Triticum baeoticum* and *T. dicoccoides*) (Figure 4.33c), as it was for the field collections (Figures 4.27c and 4.28b).

To ascertain whether differentiation of species along axis 1 (water-use efficiency) is related to genome size (as it was for the field collections, see Figure 4.27d), the same plot was recoded by genome size class (Figure 4.33d). In the case of the experiments, however, no such differentiation was apparent. There were, however, no species falling within the 'very small' range of genome sizes that characterised species with high water use efficiency in the field collections.

The species plot resulting from an analysis of the five leaf and canopy attributes for grasses (Figure 4.21b) was also recoded by domestication status (Figure 4.34b). This analysis incorporates the 2012/13 (combined) glasshouse experiments, the 2013 growth chamber experiment and the 2012 growth chamber experiments (for which canopy dimensions as well as leaf attributes are available). The first two components primarily reflect fertility (axis 1), with DMC loading positively and SLA negatively while, on the second axis, canopy height loads positively (though canopy diameter is in a relatively neutral position) (Figure 4.34a, as for Figure 4.21a). As seen in an earlier plot (Figure 4.21b), axis 1 clearly distinguishes species from the three experiments. More importantly, on axis 2, the progenitor species from all three experiments are located at or toward the top of each experimental cluster, including both CO₂ treatments within the 2013 growth chamber experiment (Figure 4.34b).

The analyses were repeated with the addition of the three domesticated cereal species in the 2013 glasshouse experiment, *Hordeum vulgare*, *Triticum monococcum* and *T. dicoccum,* (using first the leaf and stomatal attributes and then the leaf and canopy attributes). The attribute loadings on each axis remain essentially the same, and the domesticated species tend to plot with the progenitor species in both analyses (Figures 4.35 and 4.36). Like the progenitor species, the domesticated species tend to plot towards the positive (wetter) end of axis 1 in Figure 4.35b, having fewer, larger stomata than the other wild species, fall into the same genome size class as the wild progenitors (Figure 4.35d). The domesticated species are also at the positive extreme of their experimental cluster on axis 2 in Figure 4.36b, having taller canopies than the wild species in their experimental cluster, including most of the progenitor species.

Within the 2012 growth chamber experiment, *Avena sterilis* (one of likely secondary progenitor species of *A. sativa*) also plots with the primary progenitor species (Figure 4.36b).

Similarly, within the 2013 growth chamber experiment, putative progenitor species *Triticum araraticum* plots with the primary progenitor species (Figure 36b), which is in line with the results from the field collections (Figure 4.30b).

4.3.2.2 Legumes

The species plot resulting from an analysis of the five leaf and stomatal attributes for legumes (Figure 4.37d) was recoded first by domestication status (Figure 4.37b, with labelled version 4.37c), and then by genome size class (Figure 4.41b). This analysis incorporates the 2013 glasshouse and 2013 growth chamber experiments (including 'high' and 'low' CO₂ treatments), and both experiments include the three pulse progenitor species (*Cicer reticulatum*, *Lens orientalis* and *Pisum humile*), as well as the three pulse domesticates (*C. arietinum*, *L. culinaris* and *P. sativum*) that were grown in the 2013 glasshouse experiment. There is no distinction between the domesticated/progenitor species and other wild species, within either experiment or CO₂ treatment (Figures. 4.37b and 4.37c), on either axis. There is no differentiation between species of different genome sizes on axis 1 (fertility), but on axis 2, those species with very small genomes (including the *Cicer* domesticate and progenitor species) tend to plot towards the negative (bottom, drier) end of the axis (Figure 4.37d), having many, smaller stomata. This is consistent with the field collections (Figure 4.31d).

Among the progenitor and domesticated species, however, the *Cicer* species tend to plot towards the negative (bottom, drier) end of axis 2, having more, smaller stomata than the *Lens* and *Pisum* species (Figure 4.37c), and the *Cicer* species fall into the smallest genome size class, unlike the *Pisum* species (no genome data is available for the *Lens* progenitor) (Figures 4.37c and 4.37d).

The species plot resulting from an analysis of the five leaf and canopy attributes for legumes (Figure 4.26b) was recoded by domestication status (Figure 4.38b). This analysis includes only the 2013 growth experiment and again includes progenitor species *Cicer reticulatum, Lens orientalis* and *Pisum humile*. The first two components extracted primarily reflect 'fertility' (axis 1) and canopy height (axis 2) (Figure 4.38a). On axis 1 (fertility), there is no differentiation between the progenitors and wild species, for either CO₂ treatment, though the *Pisum* progenitors from both CO₂ treatments tend to plot towards the negative (left) end of the axis (Figure 38b), having higher SLA and lower DMC than the *Cicer* and *Lens* progenitors. On axis 2, most of the progenitors plot neutrally (with the exception of the *Pisum* progenitor from the 'high' CO₂ treatment, which plots positively), having similar canopy heights to most of the other wild species (Figure 4.38b).

4.3.2.3 Outcome

The results demonstrate that despite differences in plant responses to 'fertility' (SLA/DMC traits) between the experiments, the progenitor and domesticated grass species are responding consistently across the experiments, and within the CO₂ treatments. The implications of these results in relation to domestication status are discussed in the following chapter.

Chapter 5: Discussion

5.1 Introduction

The analyses have shown that despite intraspecific variation, due to plastic phenotypic responses to varying environmental conditions (both in natural habitats and between growth experiments), there are traits that are consistently shared by domesticated crops and their wild progenitors. It has also been demonstrated that these shared traits can differentiate crops and wild progenitors from other wild species, the implications of which will be discussed in the following sections. Grass and legume species differ in terms of their habitat preference (Abbo et al., 2009) and water-use efficiency (Section 4.1.1), potentially influencing early plant management strategies, and the functional differences between these two families are discussed in Section 5.2. The functional attributes of grasses and legumes are then discussed separately with regard to domestication status in Sections 5.3.1 and 5.3.2 respectively.

5.2 Functional differences between grasses and legumes

The results of the principal components analyses have demonstrated that there is a tendency for the legume species to have smaller stomata and higher stomatal density than the grass species. This difference in the stomatal attributes of grasses and legumes is consistent for both the field collections and the experimental plants. Stomata are controlled by two specialised epidermal (guard) cells (Franks and Farquhar, 2007), and stomatal attributes are used in this thesis as functional proxies for water status (reflecting the water-use efficiency). Water-use efficiency is the optimisation of photosynthetic gain relative to transpirational losses (McAdam and Brodribb, 2012) and is regulated by stomata (Hetherington and Woodward, 2003). Loss of water from the leaves through transpiration places a large selective pressure on plants to economise on the use of water, owing to a combination of high transport costs to replenish transpired water and a finite availability of water in soils (Raven, 2002, McAdam and Brodribb, 2012). Stomata also take in carbon dioxide for photosynthesis, and water loss during carbon dioxide uptake is less when there are many small stomata rather than few large ones. Differences in stomatal size and density therefore reflect differences in requirements for water for photosynthesis; species with small stomata exhibit greater water-use efficiency (Hetherington and Woodward, 2003). It follows, therefore, that species associated with dry habitats have a propensity for smaller stomata while the stomata of species associated with moister soil conditions tend to be larger (Hodgson et al., 2010). This is supported by the research presented here, where the majority of the legume species have stomatal attributes

indicating a greater ability to adapt to dry conditions, whereas the stomatal attributes of the majority of grass species indicate a greater adaptive ability to moist conditions. The results of the analyses performed on the two families therefore indicate functional differences between grasses and legumes with regard to their water management strategies and photosynthetic requirements.

The difference in water-use efficiency between grasses and legumes, observed in this thesis, is also reflected in their genome size: species that have very small genomes tend to be legumes, which have large numbers of small stomata and vice versa. The relationship between stomatal size and genome size can be explained through the correlation between cell size and genome size: in general, the greater the genome size of a species, the greater the size of its cells and, since stomata are controlled by guard cells, the larger the guard cell the larger the pore (stoma) between these cells (Beaulieu et al., 2008). The results presented in this thesis also meet the general expectations (Beaulieu et al. 2008) that the species with fewer, larger stomata will tend to have larger genomes, than those species with more numerous, smaller stomata and smaller genomes, for both grasses and legumes. Beaulieu et al. (2008, p. 981) demonstrated that, of the two major groups of flowering plants (angiosperms), monocotyledonous species (including grasses) have greater mean genome size, mean stomatal guard cell length (and epidermal cell area), and lower mean stomatal density, than eudicotyledonous species (including legumes). This has important implications in terms of a potential genetic role in determining the ecological and life-history strategy of a species and, in the context of subsistence strategies and early plant management activities, may have exerted influences in plant distribution and habitat preference. Abbo et al. (2009) discuss differences in habitat preference of the wild progenitors of cereals and pulses (e.g. oak-pistachio park-forest versus shallow/stony soils respectively), drawing on field observations by the authors and other scholars (e.g. Harlan and Zohary, 1966, Ben-Ze've and Zohary, 1973, Ladizinsky, 1975). The results of the research presented in this thesis indicate that the functional differences in stomatal traits and genome sizes of the two families provide insight into the differences in habitat preferences between grasses and legumes as mentioned by Abbo et al. (2009).

It has been shown that species with small genomes grow in more extreme environments, and that the frequency of species with large genomes is lower at both very low and very high July maximum temperatures, as well as low annual precipitation, illustrating their sensitivity to both low/high-temperatures and water stress (Knight and Ackerly, 2002). Sensitivity to temperature and water-soil relations are linked to genome size and rates of cell division, which impacts on phenology (i.e. seasonal growth in relation to climate and elevation) (Bennett, 1971, 1972, Cavalier-Smith, 2005, pp. 165-66); species whose growth peaks in summer

generally have a small genome, whereas a larger genome seems to be advantageous for species that grow mainly in the spring (Grime and Mowforth, 1982, Grime et al., 1985). Annual herbaceous species with water conservation strategies, such as legumes (with small genomes and stomata), are well adapted to withstand higher temperatures and potential water-induced stress (Grime et al., 1985, Knight and Ackerly, 2002). Conversely, for annual herbaceous species with larger genomes and stomata, such as grasses, cool season growth is a drought avoidance strategy, by completion of their life-cycle during the cooler and wetter autumn and spring seasons, thereby avoiding potential restrictions in growth due to summer temperature and precipitation regimes (Grime et al., 1985, Knight and Ackerly, 2002). The cool season growth of annual grasses is terminated by their determinate growth habit (where growth ceases at maturity), whereas the growth of legumes is indeterminate (continuous growth throughout life), which extends the vegetative and reproductive phases of growth (Abbo et al., 2009, p. 33).

Despite adaptation to cool season growth, annual grasses may still be vulnerable to droughted conditions if these are experienced early in the growing season, prior to the completion of their life cycle. Conversely, the indeterminate life history of legumes enables them to grow and fruit later in the growing season, and so potentially recover from episodes of water deficiency. Determinate growth is also accompanied by synchronous maturation which facilitates the efficient gathering of grasses over a limited time period, as compared to the extended opportunities for (albeit less efficient) collecting of legumes (Abbo et al., 2009). These biological differences may therefore influence human-decision making with regard to plant collecting. Due to the attested differences between cereals and pulses in their physiology, population structure and ecological preferences, Abbo et al. (2009) have called for research into cereal and pulse domestication to focus on the biological differences rather than similarities between the two families, in order to further current understandings of the process of domestication of the Neolithic founder crops. The analyses presented in this thesis have risen to this challenge by contributing tangible evidence of differences between grasses and legumes that relate to photosynthetic capacity, and the resource requirements associated with habitat preferences and seasonal growth habit.

5.3 Functional differences in relation to domestication status

5.3.1 Grasses

The results for grasses, from both the field collections and the experiments (at both $CO₂$ levels), show that the primary (founder) domesticated crops (barley, einkorn and emmer wheat) and their wild progenitors, share similar leaf and canopy functional attributes and stomatal traits, all having larger canopy dimensions, a greater leaf area:thickness ratio, and fewer, larger stomata, as well as larger genome size. These attributes indicate their competitive abilities, including their ability to respond to productive, fertile, moist conditions, provided soil disturbance is not too great. The other attributes relating to resource acquisition (SLA and DMC), however, are not appreciably different between domesticated/progenitor species and other wild species, perhaps suggesting that the ability to out-compete other species (through larger size) is a more important factor in their selection than resource acquisition *per se*. The larger genome and stomatal size of domesticated and progenitor species also impose seasonal constraints on the growth of domesticated crops and progenitors. Where 'lost' and secondary crop progenitors were included in analyses, they exhibited traits similar to those of the Neolithic cereal crops and progenitors. The results of this thesis are discussed here in the context of other research that uses functional ecological approaches in relation to plant domestication.

The competitive abilities conferred by the effective resource acquisition of domesticated cereals and their wild progenitors, as reflected here in canopy traits, are consistent with a number of other functional ecological studies that include other traits that also reflect a plant's response to fertility and disturbance. For example, Cunniff et al. (2014) used a functional ecological approach to test the hypothesis that the traits of the Fertile Crescent wild grass progenitors were advantageous in the fertile, disturbed habitats surrounding early settlements and in cultivated fields compared to other wild grasses that may have been available for exploitation. Testing primarily hard functional traits (such as rate of germination, relative growth rate, net assimilation rate, leaf mass ratio, resilience to defoliation and seed yield), but also soft traits (such as plant size, SLA and seed mass), Cunniff et al. (2014) found that the crop progenitors of barley, einkorn and emmer had larger seedlings, faster germination, greater seed mass, growth rate, height and yield than other wild grasses, and were also more resistant to defoliation. On the basis of this different combination of attributes, Cunniff et al. (2014) concluded that cereal progenitors had a competitive advantage over other wild species, and that this may have been amplified in situations where the productivity potential of the habitat

was increased by deliberate human activities. Deliberate activities such as fertilising during cultivation or the deposition of domestic refuse around habitation areas would both result in enhanced soil fertility, and both activities may have had the unintended consequence of favouring certain plants species that are better adapted to take advantage of increased fertility.

It is interesting to compare this with the results of experimental research conducted by Preece et al. (2015), which examined whether the wild progenitors of cereal (and pulse) crops were higher yielding than other wild species that were potentially collected. They found that, although crop progenitors tend to have larger seeds than other wild species, there was no significant difference in total seed yield per plant based on domestication status. This finding that there is no difference in yield between crop progenitors and other wild species appears to be contrary to Cunniff et al.'s (2014) earlier study, which concluded that cereal progenitors were higher yielding than other wild grasses. This apparent discord may be explained by differences in the scale of the experiments and methods used to calculate yield. Preece et al. (2015) investigated a wider range of wild grasses (21 wild species, including the three progenitor species), compared to Cunniff et al.'s (2014) nine wild grass species (as well as wild legumes). In addition, in Cunniff et al.'s (2014) experiment, the calculation of yield was based on the estimated number of seeds per plant and their average weight, whilst in the subsequent experiment conducted by Preece et al. (2015), the yield calculation was based on the actual weight of harvested seeds. This suggests that Preece et al.'s (2015) results, based on actual measurements and a larger sample, are more reliable than those of Cunniff et al. (2014). Further experimental research, using groups of the same species grown together, showed that total seed yield per unit area was also not greater for cereal progenitors than for other wild grasses (Preece et al., 2018). These results suggest that neither seed yield per plant nor area seed yield was a significant selection pressure in the domestication process (Preece et al., 2015, 2018). This is in contrast to the results indicating that progenitor species have greater competitive and resource acquisitive abilities than other wild species, indicating that these characteristics may be more important than seed yield in the process of domestication.

The differences in stomatal and genome traits of domesticated cereals and their wild progenitors compared to other wild species, identified in this thesis, indicate that water-use efficiency and soil-water status are important factors in the process of domestication. These traits reflect the sensitivity of cereal crops and their progenitors to soil water deficits compared to other wild grass species, as well as the ability of progenitors and crops to thrive in moist soil conditions. There was, however, no apparent difference between the stomatal size and density of domesticated cereals and their progenitors. Milla et al. (2013) also screened the

stomatal size, density and distribution of 24 herbaceous crops and their wild progenitors (including oat and rye but none of the primary (founder) cereal crop progenitors), grown under experimental conditions. They too found that there were no consistent differences in stomatal size and density between the herbaceous crops they studied and their wild progenitors (Milla et al., 2013). They found, however, that under domestication there is a change in the distribution of stomata, with increased density on the upper leaf surface of domesticated species (Milla et al., 2013). Stomata on the upper leaf surface are more susceptible to droughtinduced stress, due to increased stomatal conductance (Aston, 1978, Mott and O'Leary, 1984), and so the apparent shift in stomatal distribution may reflect stomatal evolution under domestication where soil-water status is more predictable (Milla et al., 2013). They propose that, in situations where water-soil relations are enhanced and predictable, for example in artificial (i.e. managed) conditions, species with larger stomata (such as the domesticated cereal crops) would be at a selective advantage. This suggests that the advantage of progenitors over other wild species in moist conditions (indicated by stomatal size and density in this thesis) is apparently further enhanced, through a different mechanism (a change in stomatal distribution), in the evolution from progenitor to domesticated species. The larger genome size of the cereal crops and their progenitors has further ecological implications in relation to seed and seedling size. Genome size tends to be positively correlated with seed mass (Marañón and Grubb, 1993, Knight et al., 2005, Beaulieu et al., 2007, Hodgson et al., 2010, p. 574), so these comparatively large-genomed domesticated and progenitor grass species are also large-seeded (Cunniff et al., 2014, Preece et al., 2015, 2017, 2018, Milla et al., 2018), and the greater seed mass of cereal progenitors confers a competitive advantage in terms of rapid germination and seedling size (Cunniff et al., 2014).

In the research presented here, the shared traits of domesticated cereals and their wild progenitors tend not to clearly separate them from the range of attribute values set by the other wild grass species. Rather, the domesticated and progenitor species tend to occupy only one part of the phenotypic range of the wild species. The exception is canopy height where, in the experiment that included the domesticated cereal species, the progenitor species were all taller than the other wild species in the experiment, and the domesticated species were all taller than their respective progenitors. This seems to indicate that large canopy size is particularly a characteristic of domesticated cereals. This is consistent with research by Preece et al. (2017) where domesticated cereal and pulse crops had on average a 40% greater plant size compared to their wild progenitors. It is also consistent with research by Milla et al. (2014) who found that competitiveness for light (as indicated by canopy height, leaf size and absolute growth rate) was greater for domesticated species than for their wild progenitors, while other

attributes, such as SLA and DMC, were not consistently associated with domesticated crop species. The overall tendency for the domesticated cereals and progenitor species to remain within the phenotypic range of the wild species, however, is consistent with the findings of Milla et al. (2018). They demonstrated that herbaceous crops (including cereals and pulses) are fast growing species (with high leaf nitrogen content), that are equipped to compete well in resource-rich environments (having tall canopies), but remain within the phenotypic range of wild herbaceous species. These results were interpreted as indicating a process of 'habitat filtering', whereby domesticated cereals are better adapted to intensively managed, highresource habitats than most wild species, which tend to be outcompeted by the domesticated species and so 'filtered out' of this type of habitat.

In sum, Neolithic domesticated cereals, their wild progenitors (and other 'lost' or secondary cereal progenitors) tend to have larger canopies than other wild grasses, providing a competitive advantage in terms of light interception in fertile, moist environments, that are not too heavily disturbed. Due to their comparatively large genome and stomatal size, however, they are subject to water-induced stress and so predisposed to complete their growth cycle early as a strategy for the avoidance of summer drought. Wild cereal progenitors tend to be towards the 'competitive' end of the spectrum for wild species generally, while domesticated cereal crops tend to be even larger, and so more competitive than their wild progenitors.

5.3.2 Legumes

The identification of differences between domesticated pulses, their wild progenitors and other wild legumes in the field collections is hampered by the small number of domesticated and progenitor species available for analysis (domesticated lentil and pea, and the wild progenitor of pea). Three pulse founder crops (pea, lentil and chickpea), and their wild progenitors were, however, included in the experiments. The domesticated and progenitor species of pea from both field collections and experiments exhibit traits similar to those of the domesticated cereal crops and their wild progenitors, tending to have larger canopy dimensions, fewer larger stomata and larger genome sizes, than other wild legumes. They also tend to have higher SLA and lower DMC values than other wild legumes, a difference that was not observed for grass species. The conclusions drawn for the cereals concerning their competitive abilities, therefore, also apply to pea, so the following discussion will focus on the other two pulse crops and their wild progenitors.

The functional attributes of chickpea domesticates and progenitors (represented only in experiments), in particular, do not exhibit the same traits as those of cereals and pea, having

smaller canopy dimensions, stomata and genome size, lower SLA and higher DMC than other wild legumes. The traits identified in domesticated chickpea and its wild progenitor (many, small stomata and very small genome size) indicate greater water-use efficiency than cereal domesticates and progenitors, and enable this species to better tolerate droughted conditions and high temperatures (Grime et al., 1985, Knight and Ackerly, 2002, Hodgson et al., 2010). Based on its smaller canopy size, however, chickpea does not have their ability to be competitive in productive (moist, fertile) habitats, and is the least competitive of the Neolithic founder crops. The results for lentil are more ambiguous (and genome data are lacking for the progenitor species). Domesticated and progenitor lentil species have a sensitivity to waterinduced stress similar to pea, having fewer, larger stomata than chickpea, as well as the larger genome size of the domesticated crop, but they are apparently less competitive (having shorter canopies) than pea. Under productive conditions, therefore, large fast-growing plants such as pea have a greater ability to acquire nutrients and resources for photosynthesis than smaller plants such as lentil and chickpea (and other wild grasses and legumes).

Previous research into the process of plant domestication using a functional ecological approach has tended to focus on cereals (e.g. Cunniff et al., 2008, 2009, 2014, 2017, Preece et al., 2018), and those that have applied such ecological principles to pulses have primarily concentrated on seed attributes (e.g. Kluyver et al., 2013, Preece et al., 2015) and reproductive attributes (Preece et al., 2017). Plant size traits (total plant height (shoot length in the case of legumes) and above-ground biomass) are, however, included in Preece et al.'s (2015, 2017) growth experiments, which does afford comparisons with the results of this thesis. The research presented here has shown that the canopy dimensions of the wild progenitor of domesticated pea were greater than those of most other wild legume species, but the canopy height of lentil and chickpea progenitors was no greater than that of other wild species. Preece et al. (2015: Table 1) found no significant overall difference in total plant height between the wild progenitors of pulses and other wild species. This probably results primarily from the amalgamation of all three progenitor species in the calculation of statistical significance, one of which (pea) has larger canopies while the others (lentil and chickpea) do not. The analyses presented here have therefore differentiated potentially contrasting strategies of pea progenitors (an ability to take advantage of fertile, moist conditions) and of lentil and chickpea progenitors, that was not apparent in earlier research.

It was not possible to compare the canopy size of domesticated lentil or chickpea with their wild progenitors in the research presented here (due to the absence of canopy size data for the domesticated species), but the canopy dimensions of domesticated pea were no greater than those of its progenitor. On the other hand, plant size, as measured by above-ground

biomass shows that domesticated pea, lentil and chickpea have on average 40% greater plant size than their wild progenitors (Preece et al., 2017), and this increase in plant size is apparent across all three progenitor species (Preece et al., 2017: Figure 3). Plant and canopy size are useful indicators of competitive ability, but neither canopy dimensions nor above-ground biomass provides a perfect measure of this: canopy height and diameter provide a measure of overall photosynthetic capacity (and may be alternative mechanisms for achieving this), while above-ground biomass is a better measurement of overall plant size (but includes reproductive as well as vegetative tissue). It is thus perhaps unsurprising that these traits sometimes give conflicting results.

5.3.3 Summary

The research presented here has indicated two 'plant strategies' that may have relevance for understanding the process of crop domestication in southwest Asia. The founder crops and their wild progenitors can be located on a spectrum from 'competitive' to 'water-use efficient' strategies. Domesticated cereal and pea crops and their progenitors fall at the competitive, resource acquisitive, end of the spectrum while domesticated chickpea and its wild progenitor are at the water-use efficient end, being the most drought tolerant and least competitive of the founder crops and progenitors. The results for domesticated lentil and its wild progenitor are more ambiguous indicating that it is potentially sensitive to water-induced stress, but not particularly competitive. The implications of these findings for the emergence of agriculture are discussed in Chapter 6.

Chapter 6: Conclusions

6.1 Introduction

This research has sought to identify the selective pressures, both natural and anthropogenic, that led to cereal and pulse domestication in southwest Asia through the identification of traits that enabled certain species to thrive in response to the ecological selection pressures associated with the climatic conditions of the Late Pleistocene/early Holocene transition and the anthropogenic environment in which domestication arose. Based on the evidence presented in this thesis, the cereal and pea founder crops and their wild progenitors have functional traits that give them a competitive advantage over most other wild grasses and legumes in fertile, moist environments. Chickpea, and to a lesser extent lentil, however, appear to possess traits that would make them less competitive (both species) but more drought tolerant (chickpea) than the cereals and pea. The following sections explore the implications of these findings for current debates concerning the origins of agriculture in southwest Asia, first in the context of pre-agrarian subsistence strategies as a precursor to agriculture (6.2.1), then in the context of agricultural events (6.2.2). Since cereals and pea share similar traits, they will be discussed first within each section, followed by a consideration of chickpea and lentil.

6.2 Implications of the plant ecological results for proposed explanations for the origins of agriculture

6.2.1 Pre-agrarian changes

It has been suggested that the impetus for hunter-gatherers to make significant changes to subsistence patterns (such as the development of agriculture) might be borne out of a disruption of the equilibrium between population and resources. This may be caused by deteriorations in the climate (Moore and Hillman, 1992, Hillman et al., 2001, Bar-Yosef, 2001, 2011, 2017), which led to the depletion of desirable food resources, or an increase in population (Cohen, 1977, 2009), either (or both) of which would lead to a population-resource imbalance, where the population exceeds the carrying capacity of the local environment (Binford, 1968). During the Late Pleistocene and early Holocene, drought would have been a major source of stress for herbaceous plants (Erskine and El Ashkar, 1993) and water the foremost limiting factor on plant growth and productivity in arid and semi-arid regions (Sairam et al., 2001, Abbo et al., 2010b). As shown here, most of the founder crops (in particular cereals and pea) and their progenitors would have been particularly vulnerable to soil water

deficits compared to other wild grasses and legumes. Explanations for the origins of agriculture that propose domestication arose in response to deteriorations in climatic conditions, such as those of the cold and arid Younger Dryas (e.g. Moore and Hillman, 1992, Hillman, et al., 2001 Bar-Yosef, 2011), would put these founder crop progenitors at a disadvantage for successful cultivation and domestication. This also has implications for other explanations relying on a population-resource imbalance, such as the diet breadth model.

The competitive characteristics of the cereals and pea are more compatible with models that emphasise the ameliorating climatic conditions of the early Holocene (i.e. warm and wet, with elevated CO₂) as a pre-requisite for the emergence of domestication (Sage, 1995, Richerson et al., 2001, Cunniff et al., 2008, 2010, Willcox et al., 2009). Whilst all plant species would have benefitted to varying degrees from the climatic amelioration associated with the early Holocene, the cereal and pea progenitors would have been at a potential advantage due to their greater photosynthetic capacity, including their facility for greater light capture and ability to take advantage of enhanced CO₂ and soil water levels. Despite potential habitat filtering that may favour competitive wild progenitor species, and possibly make them more visible to foragers, Savard et al. (2006) point out that cereal and pulse progenitors are not a significant component of archaeobotanical assemblages from pre-agricultural sites, and that other wild grasses and legumes (including small-seeded species) appear to have had greater dietary importance than the progenitor species. Arguably then, the potential prevalence of competitive cereal and pea progenitors in favourable natural habitats was not a pre-agrarian selection factor in the process of domestication.

The natural habitats of the poorly competitive wild chickpea and lentil progenitors, such as stony habitats with steppe-like vegetation, woodland clearings near parkland steppe, and gravelly hillside slopes (Abbo et al., 2008a, Fuller, 2007, Zohary et al., 2012), indicate that it was not only the more fertile, moist habitats (in which the wild cereals thrive) that were exploited for food. Plant management strategies would therefore require some level of coordination in the collection strategies for the locally abundant and competitive cereal progenitors, and the more dispersed stress-tolerant chickpea (and lentil), which would influence scheduling decisions. In fact, Blumler (1991b) suggested that pulses may have been deliberately domesticated to avoid scheduling conflicts with the harvesting of cereals. These conflicts might arise between the cereals and pea/lentil (with large genomes and an adaptation to cool season growth), which would be compatible with Blumler's (1991b) proposal, but are less likely for chickpea (with its small genome, and adaptation to warm season growth).

6.2.2 Changes within anthropogenic environments

The arrival of plants into man-made habitats (whether as 'pioneer species' or by human intention) changes the ecological selection pressures on these plants (Zohary, 2004). Within this anthropogenic environment, selection pressures are primarily driven by disturbance and enhanced soil nutrient content. Disturbance associated with human activity includes trampling, grazing and niche construction activities, such as clearance for construction purposes and opening areas for grazing livestock or cultivation, whilst the accumulation of domestic debris and the deposition of faeces in and around settlement sites leads to soil enrichment (Byrd, 2005, Yerkes et al., 2012). Human-driven selection pressures would have been further amplified by early cultivation, which may have involved tillage, fertilization and/or watering.

The competitive abilities of the barley, einkorn, emmer and pea progenitors for rapid resource acquisition in fertile, moist conditions would have put them at an advantage compared to other wild grasses and legumes, in these anthropogenic environments. The results presented in this thesis are, therefore, compatible with theories for the origins of agriculture, which suggest that domesticated crops arose from wild species that colonized the fertile, disturbed conditions associated with human activity, such as the dump-heap hypothesis (e.g. Engelbrecht, 1916, Sauer, 1952, Harlan and de Wet, 1965, Harris, 1969, Hawkes, 1969). They are also compatible with theories for the origins of agriculture that envisage a coevolutionary (mutualistic) relationship between plants and humans, such as Rindos's (1980) model and niche construction theory (Smith, 2006, 2007, 2011b, Zeder, 2012a, 2015, 2016), in which both plants and people gain benefit from an intensifying association, to the exclusion of other plants and animals. The cereal and pea progenitors' potential to take advantage of wetter conditions to achieve high biomass, at the expense of smaller, less competitive wild grasses and legumes, would also be consistent with artificial watering of cultivated plots or the location of PPN settlements near moist areas (such as alluvial grasslands) for cultivation purposes. Even so, increased precipitation associated with the onset of the Holocene would also favour the cereal and pea progenitor species.

Other aspects of the results bring into question the level of disturbance associated with the domestication of the cereals and pea. The large canopy dimensions of the cereal and pea progenitors (that distinguish them from other wild species) would give them a competitive advantage over these other species only if they were able to achieve at least some of their potential canopy size. Under particularly disturbed conditions, this would not be possible, which suggests that these progenitor species were selected in environments with only

moderate disturbance, at most. This is in line with field observations by Zohary (1969) and Blumler (1990, 1996) that wild wheat requires little or no disturbance to thrive, and is primarily adapted to ungrazed, undisturbed conditions (Zohary, 1969, Blumler, 1991a, 1991c, Noy-Meir et al., 1989, Noy-Mair, 1990, Abbo et al., 2005), though wild barley, and on occasion einkorn, grow well in disturbed habitats (Zohary, 1969, Abbo et al., 2005). Overall, therefore, it appears that fertility (and perhaps soil moisture) may have played a greater part in the selection of the progenitor species, with disturbance possibly playing a more minor role in some cases, which provides an indication of the conditions prevailing in early cultivated plots, where these species were primarily domesticated.

Explanations for the emergence of agriculture due to socio-cultural pressures tend to rely on the generation of a food surplus, in order to meet social obligations or the need for reciprocity, as a motivation for the intensification of plant exploitation leading to domestication (Bender, 1978, Hayden, 1990, 2009). While the evidence presented here does not rule out this possibility, if the domestication of these species was driven by selection within anthropogenic environments (including the cultivated plot), as suggested above, then the incentive to generate a surplus would be unnecessary as an explanation for domestication.

The progenitors of chickpea and lentil are less competitive (with smaller canopies) than the cereals, though lentil is apparently more resource acquisitive (for nutrients and especially water) than chickpea. Thus, the functional traits of the chickpea progenitor in particular (and to a lesser extent lentil) do not seem to fit explanations for the emergence of agriculture that rely on a positive response to enhanced fertility and moisture to the extent that cereals and pea do, as suggested by Blumler (1996) and Abbo et al. (2005). This implies that different selection pressures may have acted on these species during the process of domestication. Alternative suggestions for the deliberate domestication of pulses have been made by Willcox (2012a, p. 106). He suggests that wild lentil, which is ubiquitous on early agrarian sites in the Levant, may have been brought into cultivation in order to facilitate access to sufficient yields that may be difficult to achieve in natural habitats, due to its sporadic distribution and small stature. The traits of chickpea (and lentil), may then reflect what Zeder (2015, p. 2) termed a 'directed pathway' to domestication, where there was deliberate intent to domesticate a particular species in order to promote its predictability and reliability, which might be particularly necessary for uncompetitive (but otherwise desirable) species like chickpea and lentil.

Other explanations emphasise the complementarity of cereals and pulses. For example, Abbo et al. (2008b, pp. 3175-3176) proposed that the exploitation and subsequent domestication of

lentil and chickpea, which may be considered erratic and low-yielding with sporadic distribution relative to grasses (Abbo et al., 2009), was a deliberate strategy for mitigating the risks of crop failure, in addition to nutritional and cultural considerations. This thesis has demonstrated that chickpea has functional characteristics that would make it drought tolerant, and so a useful complement to drought-sensitive cereals as part of such a mitigation strategy. Zohary et al. (2012), however, have noted that archaeobotanical remains of chickpea are poorly represented compared to lentil and pea, so it is debatable whether chickpea actually fulfilled this role. The complementary adaptations to productive or unproductive conditions of cereals and pea, compared to chickpea (and possibly lentil), identified in this thesis, might also have allowed early cultivators to grow the former crops on more fertile, moist soils while chickpea (and perhaps lentil) could be grown on more nutrient poor soils. The cultivation of a range of crops that are adapted to both productive and unproductive conditions could, therefore, have potentially increased the area of land that successfully returned yields.

6.2.3 Overall summary

This thesis contributes to the growing body of research that applies ecological principles to current understandings of the process of plant domestication. It provides insights into how natural and anthropogenic selection pressures acted on wild grasses and legumes, and contributed to the evolution of crop progenitors into domesticated crops during the Late Pleistocene and early Holocene in southwest Asia. An examination of the functional traits of wild cereals and pulse species has identified natural- and human-driven selection pressures that may have resulted in particular species becoming the progenitors of domesticated cereal and pulse crops. A comparison of wild grasses and legumes demonstrates that the wild progenitors of barley, einkorn, emmer and pea were physiologically predisposed to have a competitive advantage over other wild grass and legume species under fertile, moist conditions. With increased atmospheric CO₂, increasing precipitation and warmer temperatures during the early Holocene, and the environmental conditions created incidentally by human activity and subsequently engineering (including cultivation) in the PPNA, the wild progenitors of the Neolithic founder crops were in effect primed for domestication by the PPNB. Similarly, a comparison of the functional traits of progenitors with domesticated species has indicated possible further evolutionary change. There is some evidence to suggest that selection pressures under cultivation continued to favour large competitive plants, conferring an increased ability of domesticated cereals and pea to respond positively to productive conditions compared to their wild progenitors. Being less sensitive to soil-water deficits than the cereal progenitors, chickpea (and possibly lentil) may have been selected for cultivation to mitigate against drought-induced crop failure, and the less resource-

acquisitive properties of chickpea and lentil, compared to cereals, may have enabled more nutrient-poor areas to be productive under cultivation.

The evidence presented here suggests that domestication of the founder cereal and pea crops could have been driven by their growth under productive soil conditions, which is compatible with theories that propose the origin of agriculture was the result of selection in anthropogenic environments, such as the dump-heap hypotheses (e.g. Engelbrecht, 1916, Sauer, 1952, Hawkes, 1969), human-plant co-evolutionary theories (e.g. Rindos, 1980, Zeder 2015, 2016), and niche construction theories (e.g. Smith, 2006, 2007, 2011b, Zeder, 2012a, 2015, 2016). The results of this thesis are also consistent with theories that agriculture was facilitated by the ameliorating (warm and wet) conditions of the early Holocene (e.g. Sage, 1995, Richerson et al., 2001, Cunniff et al., 2008, 2010, Willcox et al., 2009). Conversely, they are less compatible with models that hinge on the origins of agriculture being driven by responses to population-resource imbalance caused by deteriorating climatic conditions in the Younger Dryas (e.g. Moore and Hillman, 1992, Hillman, et al., 2001 Bar-Yosef, 2011), which may also undermine other theories based on a reduced availability of higher-ranked food sources (e.g. Winterhalder and Kennett, 2006). The results of this thesis are of less direct relevance to socio-cultural explanations that propose that the creation of surplus was a significant factor in the origins of agriculture (e.g. Bender, 1978, Hayden, 1990, 2009, 2010, Hayden et al., 2013). However, if domestication was driven by selection in the growing environment as suggested above, there would be no need to evoke an incentive to increase production in order to explain the origins of agriculture. Finally, the inclusion in the founder crop package of chickpea and lentil, which are less competitive and more tolerant of unproductive conditions than cereals, is compatible with theories that these species were deliberately brought under cultivation as a means to mitigate crop failure (e.g. Blumler, 1996, Abbo et al., 2005, 2008b, 2009, Willcox, 2012a, Zeder, 2015).

6.3 Future directions

In light of the research presented in this thesis, it is possible to make the following recommendations for additional research that would further advance our understanding of the process of plant domestication and early foraging patterns in southwest Asia.

1. Field collection data from target species for this thesis was partly collected on an encounter basis during collection trips in the Fertile Crescent and Europe (by the author and an earlier researcher working on the same topic), and partly derived from a database that focussed on wild (weed) species. Therefore, the field data for cereal and

pulse crops and their progenitors is limited compared to the data for other wild species. More replication of attribute data from landraces of cereal and pulse crops, and their wild progenitors, from places where they grow in southwest Asia, would greatly enhance the value of this dataset. If it is not possible to obtain collections from locations within southwest Asia (e.g. due to political circumstances), it would at least be helpful to make more field collections of domesticated landraces and progenitor species in locations with similar climates to those in the Fertile Crescent.

- 2. The dataset for pulses is smaller than that for cereals so, in order to test robustness of the results for pulses, a larger dataset would be needed. This could be achieved through the collection of attribute data from further experiments and/or field collections of wild pulse progenitors and domesticated landraces. This could also include the remaining pulse founder crop, bitter vetch (*Vicia ervilia*), which was not included in the dataset presented here. The existing wild legume and pulse data could then be reanalysed with the addition of these extra data.
- 3. This thesis focussed on vegetative traits relating to the growth of plants, but data on reproductive traits (including seed yield, seed size and, for grasses, number of tillers) were also collected alongside the leaf, canopy and epidermal trait data used in this thesis. Flowering traits (onset and duration of flowering) could also be acquired from regional Floras, to add to the reproductive trait dataset. Direct comparison of these reproductive traits with the vegetative traits considered in this thesis could shed light on whether the growing plant in the anthropogenic environment, or selection for food maximization, best explain the selection of progenitor species and their subsequent evolution into domesticated crops.
- 4. This thesis has demonstrated that the founder crops and their wild progenitors (notably cereals and pea) have traits that should give them a competitive advantage over other southwest Asian wild grasses and legumes in fertile, moist habitats, and that their tolerance of disturbance is limited. In order to test these ideas, growth experiments could be conducted (either in field plots located in southwest Asia or under controlled greenhouse conditions) comparing the responses of domesticated crops, their progenitors and other wild species to different levels of fertility, soil moisture content, and disturbance.
- 5. The trait-based approach used in this thesis could also be applied to gain greater insights into pre-agrarian foraging patterns, in particular scheduling decisions, and the continued importance of wild plant foraging, which persisted alongside cultivation and agriculture during the PPN. For example, existing trait data (genome size) of wild herbaceous species that were exploited for consumption, in combination with

flowering traits (notably onset and duration of flowering), may reflect seasonal exploitation of wild resources, or the use of wild resources to fill a lean season in the agricultural cycle.

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Functional attributes as a tool for understanding the process of cereal and pulse domestication

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Volume 2

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Functional attributes as a tool for understanding the process of cereal and pulse domestication

Volume 2

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Chapter 1: Tables

Table 1.1 Major differences between southwest Asian grain legumes and grasses in respect to both wild progenitors and their respective cultigens.

Reproduced from source: Abbo et al. (2009: Table 1).

Chapter 2: Tables

Table 2.1 Chrono-cultural and climatic summary of the Late Pleistocene/early Holocene transition.

Sources for environmental period dates: Weaver et al. (2003); van der Plicht et al. (2004); Broecker et al. (2010); source for cultural periods: Maher et al. (2011: Table 1 - Mediterranean and Arid Zone groups); Goring-Morris et al. (2009: Table 10.1 - Upper Tigris Region).

Table 2.2 List of the seven Neolithic 'founder' cereal and pulse crops and their progenitors (following Zohary et al., 2012).

Table 2.3 List of potentially additional cereal and pulse crops and their wild progenitors (following Fuller et al., 2012: Table 1, Abbo et al., 2013a).

Chapter 3: Tables
Table 3.1 The functional attributes used and their ecological significance (modified from Jones et al., 2010: Table 1).

(c) Attributes relating to the capacity to regenerate under conditions of high disturbance

Table 3.3 Collections from Haute Provence, France, field trip, May 2013.

Table 3.4 List of collections for which trait data were extracted, from the functional ecological database within the University of Sheffield.

Table 3.5 List of collections for which trait data were extracted, from the functional ecological database developed within the Unversity of Oxford.

Developed by researchers within the University of Oxford (PI Amy Bogaard, University of Oxford, in conjunction with researchers Mike Charles, University of Oxford, Glynis Jones, Department of Archaeology, University of Sheffiled, and John Hodgson, Unit of Comparative Plant Ecology, Department of Animal and Plant Sciences, University of Sheffield).

aegicyl100301 1003 Aegilops cylindrica Wild Southern Provence, aegicyl Poaceae France Europe Wild aegicyl100302 1003 Aegilops cylindrica Southern aegicyl Poaceae Provence, France Europe Wild aegitri100301 1003 Aegilops triuncialis Southern aegitri Poaceae Provence, France Europe 1003 Wild bromcom100301 Bromus commutatus Provence, Southern bromcom Poaceae France Europe 1003 Cicer arietinum ciceari100301 Fabaceae Provence, Southern ciceari Dom France Europe eleuind Wild eleuind100301 1003 Eleusine indica Poaceae Provence, Southern France Europe Wild lathhir lathhir100301 1003 Lathyrus hirsutus Fabaceae Provence, Southern France Europe Wild lathhir lathhir100302 1003 Lathyrus hirsutus Fabaceae Provence, Southern France Europe Wild lathhir lathhir100303 1003 Southern Lathyrus hirsutus Fabaceae Provence, France Europe lathset lathset100301 1003 Wild Lathyrus setifolius Fabaceae Southern Provence, France Europe lenscul100301 1003 Lens culinaris culinaris Southern lenscul Fabaceae Dom Provence, France Europe
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France Europe
trifarv trifarv100301 Trifolium arvense 1003 Fabaceae Wild Southern Provence,
France Europe
trifinc trifinc100301 1003 Trifolium incarnatum Fabaceae Wild Southern Provence,
France Europe
incarnatum
trifstr trifstr100301 Wild Southern 1003 Trifolium striatum Fabaceae Provence,
France Europe
tritmon tritmon100301 1003 Southern Triticum monococcum Poaceae Dom Provence,
France Europe
vicinar100301 Wild vicinar 1003 Vicia narbonensis Fabaceae Provence, Southern
Europe France

Table 3.6 List of the grass species and accessions used in the 2013 Glasshouse experiment, including the seed bank it was obtained from and country of origin.

Seed material was obtained from the USDA Germplasm Resources Information System (GRIN), the Millennium Seed Bank (MSB) Seed List and IPK Gaterslaben Genebank (IPK).

*Indicates putative progenitor status.

Table 3.7 List of the legume species and accessions used in the 2013 Glasshouse experiment, including the seed bank it was obtained from and country of origin.

Table 3.8 List of the grass species and accessions used in the 2013 Growth chamber experiment, including the seed bank it was obtained from and country of origin.

Seed material was obtained from the USDA Germplasm Resources Information System (GRIN), the Millennium Seed Bank (MSB) Seed List and IPK Gaterslaben Genebank (IPK). *Indicates putative progenitor status.

Table 3.9 List of the legume species and accessions used in the 2013 Growth chamber experiment, including the seed bank it was obtained from and country of origin.

Table 3.10 List of the grass species and accessions used in the 2012 Glasshouse experiment, including the seed bank it was obtained from and country of origin.

Seed material was obtained from the USDA Germplasm Resources Information System (GRIN) and IPK Gaterslaben Genebank (IPK).

*Indicates putative progenitor status. *Indicates putative progenitor status and ~indicates secondary domesticate/progenitor status.

Table 3.11 List of the grass species and accessions used in the 2012 Growth chamber experiment, including the seed bank it was obtained from and country of origin.

Seed material was obtained from the USDA Germplasm Resources Information System (GRIN), the Millennium Seed Bank (MSB) Seed List and IPK Gaterslaben Genebank (IPK) (seedlings courtesy of G. Frenck)

Chapter 4: Tables

Table 4.1 One-tailed paired t-tests for the grass species field collections (using species mean attribute values for Northern Europe, Southern Europe and Near Eastern field collections).

Bold type indicates significant differences (*p*<0.05 in one-tailed paired t-test).

Table 4.2 One-tailed paired t-tests for the legume species field collections (using species mean attribute values for Northern Europe, Southern Europe and Near Eastern field collections).

Bold type indicates significant differences (*p*<0.05 in one-tailed paired t-test)

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Table 4.3 One-tailed paired t-tests for the 2013 growth chamber experiment grass species (using species mean attribute values for Late Epipalaeolithic ('low') and current ('high') CO₂ treatments).

Bold type indicates significant differences (*p*<0.05 in one-tailed paired t-test).

Table 4.4 One-tailed paired t-tests for the 2013 growth chamber experiment legume species (using species mean attribute values for Late Epipalaeolithic ('low') and current ('high') CO₂ treatments).

Bold type indicates significant differences (*p*<0.05 in one-tailed paired t-test).

Chapter 1: Figures

Figure 1.1 Map of southwest Asia showing the geographical extent of the Fertile Crescent. Map courtesy of E. Forster.

Chapter 2: Figures

Figure 2.1 Topography of southwest Asia. Image courtesy of E. Forster: Digital elevation map created using the ASTER GDEM, which is a product of METI and NASA. Information and images were obtained from site http://lpdaac.usgs.gov/get_data maintained by the NASA Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota, 2012.

Figure 2.2 Soil map of southwest Asia. Image courtesy of E. Forster: source FAO/IIASA/ISRIC/JRC (2012).

Figure 2.3 Köppen-Geiger climatic classifications for southwest Asia. Figure modified from sources: https://people.eng.unimelb.edu.au/mpeel/Koppen/Europe_MiddleEast.jpg; https://sos.noaa.gov/datasets/koppengeiger-climate-classification-2007; and Peel et al. (2007), the latter under a Creative Commons Attribution-ShareAlike license: http://creativecommons.org/licenses/by-sa/4.0/.

Figure 2.4 Recent mean annual precipitation in the region of the Fertile Crescent, southwest Asia. Image courtesy of E. Forster: Map created using data from the Worldclim website, data source Hijmans et al. (2005).

Figure 2.5 High Resolution Köppen-Geiger Classifications of Paleoclimate Simulations. Figure modified from source: Willmes et al. (2017: Figure 2), © 2016 John Wiley & Sons Ltd.

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Figure 2.7 Map of the Pre-Pottery Neolithic sites in southwest Asia with archaeobotanical remains included in the Origins of Agriculture database (following Wallace et al., 2019: Figure 1). Central Anatolian sites—1: Hacılar, 2: Erbaba, 3: Çatalhöyük East, 4: Can Hasan III and 5: Aşikli Höyük. Cypriot sites—6: Mylouthkia, 7: Ais Yiorkis and 8: Kastros. Southern Levantine sites—9: Hayonim Cave, 10: Yiftahel, 11: Nahal Oren, 12: Kebara Cave, 13: Atlit-Yam, 14: Gilgal, 15: Netiv Hagdud, 16: Jericho, 17: Nahal Hemar, 18: Wadi Faynan 16, 19: Shkarat Msaied, 20: Beidha, 21: Ayn Abu Nukhayla, 22: Tell Ramad, 23: Gesher Benot Yaaqov, 24: Ohalo II, 25: Gesher, 26: Wadi al-Hammeh 27, 27: Iraq ed-Dubb, 28: Ain Ghazal, 29: Wadi el-Jilat 13, 30: Wadi el-Jilat 6 & 7, 31: Zahrat adh-Dhra 2, 32: el-Hemmeh, 33: Wadi Fidan A, 34: Wadi Fidan C, 35: Basta I, 36: Tell Ghoraifé, 37: Tell Aswad, 38: Dhuweilla and 39: Azraq 31. Northern Levantine sites—40: Tell Ain el-Kerkh, 41: Tell Ras Shamra, 42: Tell Qaramel, 43: Tell Abr, 44: Dj'ade, 45: Halula, 46: Jerf el Ahmar, 47: Mureybet, 48: Abu Hureyra, 49: Douara Cave, 50: Cafer Höyük, 51: Gritille, 52: Nevali Çori, 53: Göbekli Tepe, 54: Tell Sabi Abyad II, 55: El Kowm I & II, 56: Çayönü and 57: Tell Bouqras. Sites of the eastern Fertile Crescent—58: Hallan Çemi, 59: Demirkoy, 60: Kortik Tepe, 61: Tell Maghzaliyeh, 62: Qermez Dere, 63: Yarym Tepe, 64: Nemrik 9, 65: Mlefaat, 66: Jarmo, 67: Chogha Golan, 68: Sheikh-e Abad, 69: Chia Sabz, 70: Tepe Ali Kosh, 71: Ganj Dareh Tepe, 72: Tepe Abdul Hosein and 73: Chogha Bonut. Figure courtesy of E. Forster.

Chapter 3: Figures

Figure 3.1 Map showing the extent of the Fertile Crescent (yellow shading) and the location of Bestansur Neolithic mound, Iraqi Kurdistan. Image courtesy of E. Forster.

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https://sos.noaa.gov/datasets/koppen-geiger-climate-classification-2007/; Peel et al. (2007) under a Creative Commons Attribution-ShareAlike license: http://creativecommons.org/licenses/by-sa/4.0/ and Bogaard et al. (2016a: Figure 2) under a Creative Commons Attribution license: http://creativecommons.org/licenses/by/4.0/.

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Figure 3.13 Photograph of the randomised pots of grass and legume species grown for the 2013 growth chamber experiment (July 2013), at the Sir David Read Controlled Environment Facility, University of Sheffield, UK. Image by author.

Figure 3.14 Photograph of the randomised blocks of grass monocultures grown for the 2012 glasshouse experiment (September 2012), at the Arthur Willis Environment Centre, University of Sheffield, UK. Image by author.

Figure 3.15 Photograph of the randomised pots of grass species grown for the 2012 growth chamber experiment (November 2012), at the Sir David Read Controlled Environment Facility, University of Sheffield, UK. Image by author.

Chapter 4: Figures

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b

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b

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Figure 4.31 PCA of the leaf and stomatal attributes and field collection (non-regional) species attribute means – legumes (axes 1x2): (a) plot of functional attributes, (b) plot of species, coded by domestication status, (c) plot of functional attributes, (d) plot of species by genome class. Progenitor species code: 'pisuela' = *Pisum elatius*.

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Figure 4.33 continued PCA of the leaf and stomatal attributes and experimental species attribute means, excluding domesticated species – low and current $pCO₂$ grasses (axes 1x2): (c) plot of species coded by experimental source and domestication status with labels, (d) plot of species coded by genome size class. Progenitor species codes: 'hordspo' = *Hordeum spontaneum*; 'tritbae' = *Triticum baeoticum*; 'tritdicc' = *Triticum dicoccoides*.

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Figure 4.35 continued PCA of the leaf and stomatal attributes and experimental species attribute means – grasses (axes 1x2): (c) plot of species coded by experimental source and domestication status, with founder domesticated and progenitor, and non-founder progenitor species labelled, (d) plot of species coded by genome size class. Domesticated and progenitor species codes: 'hordvul' = *Hordeum vulgare*; 'tritmon' = *Triticum monococcum*; 'tritdicm' = *Triticum dicoccum*; 'hordspo' = *Hordeum spontaneum*; 'tritbae' = *Triticum baeoticum*; 'tritdicc' = *Triticum dicoccoides*; 'tritara' = *Triticum araraticum*; 'tritura' = *Triticum urartu.*

Figure 4.36 PCA of the leaf and canopy attributes and experimental species attribute means, including domesticated species – grasses (axes 1x2): (a) plot of functional attributes, (b) plot of species, coded by experimental source and domestication status. Domesticate and progenitor species codes: 'hordvul' = *Hordeum vulgare*; 'tritmon' = *Triticum monococcum*; 'tritdicm' = *Triticum dicoccum*; 'hordspo' = *Hordeum spontaneum*; 'tritbae' = *Triticum baeoticum*; 'tritdicc' = *Triticum dicoccoides*; 'tritara' = *Triticum araraticum*; 'tritura' = *Triticum urartu*.

Figure 4.37 PCA of the leaf and stomatal attributes and experimental species attribute means, including domesticated species – legumes (axes 1x2): (a) plot of functional attributes, (b) plot of species, coded by experiment source and domestication status, (c) plot of species coded by experimental source and domestication status, with founder domesticated and progenitor, and non-founder progenitor species labelled, (d) plot of species coded by genome size class.

Figure 4.37 continued PCA of the leaf and stomatal attributes and experimental species attribute means – legumes (axes 1x2): (c) plot of species coded by experimental source and domestication status, with founder domesticated and progenitor labelled, (d) plot of species coded by genome size class. Domesticated and progenitor species codes: 'pisusat' = *Pisum* sativum; 'pisuhum' = *Pisum humile*; 'lenscul' = *Lens culinaris*; 'lensori' = *Lens orientalis*; 'ciceari' = *Cicer arietinum*; 'ciceret' = *Cicer reticulatum*.

Figure 4.38 PCA of the leaf and canopy attributes and experimental species attribute means – legumes (axes 1x2): (a) plot of functional attributes, (b) plot of species, coded by experiment source and domestication status. Progenitor species codes: 'pisuhum' = *Pisum humile*; 'lensori' = *Lens orientalis*; 'ciceari' = *Cicer arietinum*.

Appendix A

Table A.1 List of all grass species referred to in this thesis and accepted nomenclature. Sources: WCSP (2017) – retrieved 20/07/17 and 23/07/17, and Zohary et al. (2012).

Table A.2 List of legume species referred to in this thesis and accepted nomenclature. Sources: The Plant List (2013) – retrieved 20/07/17 - 24/07/17, and Zohary et al. (2012).

Appendix B

Table B.2 Functional attribute data from the 2013 Glasshouse experiment. CO₂ levels: 'Modern' relates to present day levels (c. 38 Pa).

Table B.5 Functional attribute data from the 2012 Growth chamber experiment. CO₂ levels: 'Modern' relates to present day levels (c. 38 Pa).

