Research in Context

The domestication syndrome in vegetatively-propagated field crops

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Abstract

BACKGROUND. Vegetatively propagated crops are globally significant in terms of current agricultural production, as well as in terms of understanding the long-term history of early agriculture and plant domestication. Today, significant field crops include sugarcane (*Saccharum officinarum*), potato (*Solanum tuberosum*), manioc (*Manihot esculenta*), bananas and plantains (*Musa* cvs.), sweet potato (*Ipomoea batatas*), yams (*Dioscorea* spp.) and taro (*Colocasia esculenta*). In comparison to sexually-reproduced crops, especially cereals and legumes, the domestication syndrome in vegetatively-propagated field crops is poorly understood.

AIMS AND SCOPE. Here, a range of phenotypic traits potentially comprising a syndrome associated with early domestication of vegetatively-propagated field crops is proposed, including: mode of reproduction, yield of edible portion, ease of harvesting, defensive adaptations, timing of production and plant architecture. The archaeobotanical visibility of these syndrome traits is considered with a view to the reconstruction of the geographical and historical pathways of domestication for vegetatively-propagated field crops in the past.

CONCLUSIONS. Although convergent phenotypic traits are identified, none are ubiquitous and some are divergent. In contrast to cereals and legumes, several traits seem to represent varying degrees of plastic response to growth environment and practices of cultivation, as opposed to solely morphogenetic 'fixation'.

Keywords: asexual (clonal) reproduction, vegetative propagation, phenotype, domestication syndrome, developmental plasticity, archaeobotanical visibility

The significance of vegetatively-propagated plants

Vegetatively-propagated plants are among the world's most important subsistence and commercial crops, especially in the wet tropics and subtropics. Globally significant foods that are vegetatively-propagated include bananas and plantain (*Musa* cvs), manioc (cassava, *Manihot esculenta*), potato (*Solanum tuberosum*), sugarcane (*Saccharum officinarum*), sweet potato (*Ipomoea batatas*), taro (*Colocasia esculenta*) and yams (*Dioscorea* spp.) (Figure 1). Other important vegetatively grown crops include arrowroot (*Maranta arundinacea*), old cocoyam (*Xanthosoma sagittifolium*), ginger (*Zingiber officinale*) and turmeric (*Curcuma longa*).

In this paper, we propose a domestication syndrome of convergent evolutionary traits for vegetatively-propagated crops, namely, bananas, cane grasses and root crops ordinarily grown in cultivated plots or fields. Definitions of domestication syndrome vary considerably; some are general and refer to a suite of traits that mark a crop's divergence from its wild ancestor(s). The suite includes traits that are desirable to humans, yet are not necessarily beneficial to the plant, and need not be uniform from species to species (Meyer et al 2012). Other definitions are more restrictive and link the collection of phenotypic traits associated with domestication to genetic changes in the domesticated crop relative to its wild progenitor (Gepts 2004; Allaby 2014). Although domestication syndromes are sometimes considered fixed by genetic changes (Zohary 1984; Ladizinsky 1985; Lenser and Theißen 2013; Martinez-Ainsworth and Tenaillon 2016; Kistler et al. 2018; Pickersgill 2018), this may not be an absolute requirement because the genetic correlates for phenotypically-expressed traits are not known for most crops (Smýkal et al. 2018), while in other cases they need not be present.

The domestication histories and status of several vegetatively-propagated plants are confounded because no known wild ancestor exists, for example, greater yam (*D. alata*) and sweet potato (*I. batatas*; Muñoz-Rodríguez et al. 2018). In other cases, little is known about the ecology, genetics and cultivation history of plants that were probably once important staples and now widely spread geographically, such as *Alocasia macrorrhizos* and *Xanthosoma* spp. (Brown 2000). For these crops, inferences regarding domestication history can only be drawn from present-day plants.

For domesticates descended from a wild conspecific ancestor, genetic analyses of modern and historic populations can assist in the interpretation of origins, yet most studies are limited by sampling coverage, a bias towards major cultivar groups, and genetic reshuffling through time (Roullier et al. 2013). Other domesticates are true cultigens; they are products of introgression, namely inter-specific or intra-subspecific hybridisation reflecting sexual reproduction, such as AA diploid banana cultivars (*Musa* cvs.), sugarcane (members of *Saccharum* complex) and potatoes (members of *Solanum brevicaule* complex). Diploid hybrids presumably preceded the generation of sterile, vegetatively-propagated cultivars, including several major triploid banana cultivar groups (Perrier et al. 2011) and sugarcane polyploids (Grivet et al. 2004).

For context, we initially provide an overview of the significance of different modes of reproduction for the emergence of agriculture across the globe. As a means of bridging the gaps in knowledge for the domestication of sexually and asexually-reproducing crop plants, we characterise asexual reproduction in plants and different types of vegetative propagation practice. We then present several domestication syndrome traits for vegetative crops, namely, the behavioural, physical and chemical traits that emerged as a result of human selection under early forms of cultivationand are common to derived cultivars. We then consider the

archaeobotanical visibility of these phenotypic traits for reconstructing the domestication of vegetatively-propagated plants in the past.

Early agriculture and modes of reproduction

Early and later forms of agriculture vary in their reliance on sexual and asexual modes of reproduction (Figure 1; Sauer 1952; Harlan 1971; Harris 1977; Ladizinsky 1998; Piperno and Pearsall 1998; Zohary and Hopf 2000; Denham et al. 2007).

Cultivation based on sexual reproduction through the planting of fertilised seed is commonly associated with annuals, especially cereals and legumes, as well as a broad range of oil seeds, soft-stemmed fruits and vegetables. Several globally significant cereals, in terms of modern production, contributed to early forms of regional agriculture (Fuller et al. 2014): maize (*Zea mays*) in Mesoamerica; rice (*Oryza sativa*) in southern China and Southeast Asia; wheat (*Triticum* spp.), oats (*Avena sativa*) and barley (*Hordeum vulgare*) in Southwest Asia; sorghum (*Sorghum bicolor*) in East Africa; pearl millet *(Pennisetum glaucum)* in West Africa; and, broomcorn millet (*Panicum miliaceum*) and foxtail millet (*Setaria italica*) in northern China. Other cereals and pseudocereals were incorporated into regional farming practices: *Panicum sumatrense, Brachiaria ramosa* and *Paspalum scrobiculatum* in India (Murphy and Fuller 2017); buckwheat (*Fagopyrum esculentum*) on the Tibetan plateau (Hunt et al. 2018); quinoa (*Chenopodium quinoa*) in the Andes (Bruno 2009); and pitseed goosefoot (*Chenopodium berlandieri*) in the Mississippi Basin (Smith and Yarnell 2009). Legumes were also domesticated as part of these early cultivation practices, including: peas (*Pisum sativum*; Trněný et al. 2018), chickpea (*Cicer arietinum*: van Oss et al. 2015) and lentil (*Lens culinaris*; Sonnante et al. 2009) in Southwest Asia; beans (*Phaseolus* spp.) in the Americas

(Rendón-Anaya et al. 2017); soybeans (*Glycine max*) in China (Lee et al. 2011; Zong et al. 2017); cowpea (*Vigna unguiculata*) in Africa (D'Andrea et al 2007); and, multiple pulses including mungbean (*Vigna radiata*), horsegram (*Macrotyloma uniflorum*) and pigeon pea (*Cajanus cajan*) in India (Fuller and Harvey 2006; Fuller and Murphy 2018; Fuller et al. 2019).

A domestication syndrome of convergent evolutionary traits has been proposed for many of these sexually-reproduced crops (Harlan et al. 1973; Hammer 1984; Vaughan et al. 2007; Meyer et al. 2012; Fuller et al. 2014). For some researchers a single key trait, such as loss of wild-type seed dispersal, has been singled out as *the* only marker of domestication (e.g. Zohary 1984; Abbo et al. 2014), with other changes considered to be more loosely related to plant evolution under cultivation. However, such an approach presupposes the nature of past human-plant interactions rather than inferring those interactions from empirical evidence. Given that any crop population will be undergoing selection for multiple traits at any one time, including the potential for previously unrecognized targets of selection (Vaughan et al. 2007), a broader conception of a domestication syndrome is useful as it offers multiple proxies for documenting the process of coevolution between crops and humans.

The major mechanisms of domestication inferred from archaeological remains have been determined from detailed studies of the phenotypes (macrobotanical and microbotanical) and, more recently, genotypes (ancient DNA) of a subset of sexually-reproducing crops, primarily cereals (Allaby et al. 2018; Kistler et al. 2018; Schreiber et al. 2018; Stitzer and Ross-Ibarra 2018) and legumes (Smýkal et al. 2015; Bitocchi et al. 2017). Clear physical changes in morphological architectures associated with reproduction and propagation, namely non-shattering rachis of barley (*Hordeum vulgare*; Figure 2), wheat (*Triticum* spp.; Tanno and Wilcox 2012) rice (*Oryza sativa*; Fuller et al. 2009; Barron et al. 2017) or sorghum (Winchell

et al 2017), as well as the rapid evolution of the cob in maize (*Zea mays*; Piperno and Pearsall 1998; Stitzer and Ross-Ibarra 2018), have been documented.

In comparison, there is limited archaeobotanical, ecological and genetic information regarding the phenotypic trajectories of domestication for vegetatively-propagated crops. Yet, an examination of 203 crop species, including 115 vegetatively-propagated crops, found between five and seven domestication syndrome traits with an average of 2.8 traits per species (Meyer et al. 2012). Vegetatively-propagated root crops did not exhibit significantly fewer traits than annual seed crops.

Early farming emerged in several regions based on the vegetative-propagation of staple crops that today are globally significant, most notably the Americas – manioc (*M. esculenta*), potato (*S. tuberosum*) and sweet potato (*I. batatas*) (Ugent and Peterson 1988; Piperno and Pearsall 1998) - and the Indo-Pacific region extending from eastern India to New Guinea – aroids (Aracaeae), bananas (*Musa* cvs.), sugarcane (*Saccharum officinarum*) and yams (*Dioscorea* spp.) (Burkill 1935; Li 1970; Yen 1973). Thus, despite sexually reproduced plants being at the forefront of most archaeobotanical research on plant domestication, understanding vegetative propagation is equally significant for a more complete and balanced perspective on human selection and early domestication.

Vegetative propagation is especially important for unravelling the history of early cultivation and domesticatory practices in the wet tropics and subtropics, mountainous regions, wetland habitats and deserts (Harris 1972). For instance, several regionally important crop plant assemblages are based on vegetative principles: potato (*S. tuberosum*), oca (*Oxalis tuberosa*), ulluco (*Ullucus tuberosus*) and mashua (*Tropaeolum tuberosum*)in the Central Andes (National Research Council 1989); enset (*Ensete ventricosum*) and yam (*Dioscorea cayenensis*) in Ethiopia (Hildebrand 2007; Borrell et al. 2019); plantain (*Musa* cvs.),

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Plectranthus spp., taro (*C. esculenta*) and yams (*D. rotundata-cayenensis* complex) in western Africa (Fuller and Hildebrand 2013); aroids (*Alocasia macrorrhizos, Amorphophallus paeonifolius, C. esculenta, Cyrtosperma merkusii*) and swamp sago (*Metroxylon sagu*) in the Indo-Pacific (Ruddle et al. 1978; Brown 2000; Santosa et al. 2017); and, bananas (*Musa* cvs.), taro (*Colocasia esculenta*) and yams (*Dioscorea* spp.), together with edible cane grasses (*Saccharum officinarum, Saccharum edule* and *Setaria palmifolia*) in the New Guinea region (Barrau 1955; Yen 1973; Denham 2018).

Vegetatively-propagated crops are often characterised as being of local or regional significance, as well as lacking expansive capacity (Harris 2002). Yet at the time of European exploration of the globe from the fifteenth century onwards, vegetatively-propagated crops had the widest longitudinal ranges of any food crops in the world: bananas (*Musa* cvs) were distributed across the 'Old World', from West Africa and Iberia to eastern Polynesia (Mbida et al. 2001; Dozy 1961 and Yen 1973, respectively); and, taro (*C. esculenta*) spread from uncertain homelands in Southeast Asia, eastwards into Polynesia and westwards to the eastern Mediterranean where it was known by the ancient Greeks and Romans (Grimaldi et al. 2018). As yet, the complex histories of domestication and prehistoric dispersal for many vegetatively-propagated food crops are poorly understood largely as a result of low archaeobotanical visibility and poor preservation, as well as the limited phenotypic and genetic characterisation of ancient and modern plants from wild and domesticated sources. Most interpretations rely heavily on genetic inferences from modern populations with only limited archaeobotanical support, such as for manioc (Wang et al. 2014), potato (Hardigan et al. 2017), taro (Chaïr et al. 2016) and some yams (Scarcelli et al. 2019); an exception is the banana which is present in many archaeological phytolith records (Figure 2; Perrier et al. 2011).

Asexual reproduction in plants

Many plants have two modes of reproduction: sexual reproduction from fertilised seed; and, asexual reproduction, clonal growth through regeneration from plant structures (Stebbins 1950; Harper 1977; Abrahamson 1980). Asexual reproduction bypasses pollination and production of fertilised seed; instead, genetically identical offspring to the parent plant, namely clones, are produced that are more akin to growth than to reproduction (Abrahamson 1980: 89). In trying to characterise the non-equivalence of asexual and sexual reproduction, genetically distinct individuals in a population can be considered as *genets*, while the genetically identical individuals arising from asexual reproduction of a genet are *ramets* (Harper 1977; Abrahamson 1980)

Asexual reproduction in plants occurs in two principal forms: agamospermy and vegetative reproduction (Abrahamson 1980). Agamospermy is parthenogenic seed production, also referred to as apomixis (Silverton 2008: 157). Apomictic seeds are clones of the mother plant that are packaged and dispersed in the trappings of sexually produced progeny (Silverton 2008: 457-458). They differ from *ramets* in that they still go through the same developmental program (seedling, juvenile and reproductive adult stages) as any other seed propagation cycle. Manioc is capable of apomixis (Ellstrand 2003: 80), but it is not a major reproductive strategy for any major crop plant discussed here.

Advantages of vegetatively reproduced offspring include loss of juvenility, rapid development and higher growth rates compared to seedlings because propagules are better provisioned initially with a larger food supply (Table 1; Abrahamson 1980: 96) and may even start as miniature versions of the parent plant with developed root systems (Silverton 2008:

157). Amongst flowering plants, vegetative reproduction is a low-risk adaptation in certain environments for proliferating the genet through the production of independent and hardy ramets (Table 1; Abrahamson 1980: 96). Through vegetative reproduction, individual genetic lineages may be extremely long-lived; the aspen (*Populus termuloides*) colony in southern Utah, known colloquially as 'Pando', is c. 8,000-10,000 years old (Mock et al. 2008: 4828).

The frequency of plants capable of vegetative reproduction is highly variable in different flora. Ecosystems where vegetative reproduction is noted include: high latitudes, such as boreal forests; high altitudes, where some species may lose the ability to sexually reproduce; aquatic habitats containing species that vegetatively reproduce via bulbs, corms and rhizomes, and where the fragmentation of stems and stolons can take over the dispersal function of seeds; and, habitats prone to fire in which strong vegetative reproducers employ a 'sit and wait' strategy with fast growth to recolonise newly burned habitat (Abrahamson 1980: 93; Eckert 2002). In the wet tropics, sexual reproduction is more common than asexual reproduction (Abrahamson 1980: 92), though asexual reproduction is a significant strategy for many species important to people.

Pathways to domestication

The domestication of vegetative crops, like many sexually reproduced crops, is unlikely to have been a single capture event (McKey et al. 2010). In considering the pathways to domestication of clonally propagated plants, numerous anthropic selective processes would have operated on exploited plants within a landscape, including direct selection of favoured phenotypes (which may have included translocation of whole plants or plant parts capable of reproduction, e.g., yam heads), as well as indirect processes of selection: modification of local environments through clearing and burning; modification of the immediate growth environment, such as disturbance of soils to increase looseness and friability; and, the

creation of anthropic habitats favouring particular phenotypes (Yen 1989; Hather 1996; Terrell et al. 2003; Harris 2007; Barton and Denham 2018). In all of these pathways there exists potential for phenotypic change to occur and accumulate over short and prolonged time periods through either genetic changes, involving some degree of sexual recombination or mutation, or through more immediate genetic expressions within changed ecological conditions that influence the 'plasticity' of growth form (de Kroon et al. 1994: 125-126).

As vegetative propagators, humans have acted as important dispersal agents of desired genets, moving ramets that would often only disperse locally through spreading roots, stolons and suckers adjacent to the parent. Globally, people have introduced genets into new ecological zones and regions, such as the dispersal of major cultivars, while regionally people moved plants into places of lower plant density with reduced competition, such as the translocation of yams from the Ethiopian lowlands where they occur wild to higher elevations where they do not (Hildebrand 2007). An important advantage of vegetative propagation, for both humans and plants, is independence from external pollination, such that plants are able to colonise new habitats outside of the natural range in which flowering occurs and where pollinators are absent (Abrahamson 1980: 963). It also has the potential to remove plants from natural pests (Chen et al. 2018), thereby increasing survival rates and vigour. In dispersing plants and plant parts, whether deliberately or inadvertently, such events were probably important mechanisms in plant domestication through the generation of asexually-reproducing phenotypes (outside of natural range), new phenotypes of individual species, and through the spontaneous creation of new hybrids of related species, i.e. sympatric hybridisation (Clement et al. 2010).

Arguably, vegetative propagation enables more controlled selection of favoured characteristics than under sexual reproduction. In general terms, species or specific

phenotypes of a species have been selected based on: ease of growth, hardiness and resistance to stress (whether disease, pest or environmentally-induced); productivity (including caloric, protein and oil yield, synchronicity of yield, and inter-annual reliability of production); ease of processing (such as hard seed coat or nut casing, extraction of edible portion, spininess); ease of cooking (pounding, soaking, heating, roasting, etc.); and, selection for secondary characteristics such as toxicity, acridity, colour, palatability and texture (McKey et al. 2012; Meyer et al. 2012; Smýkal et al. 2018).

The domestication syndromes of vegetatively-propagated crops

Despite the complicated and poorly documented domestication histories of most vegetatively-propagated plants, some common phenotypic characteristics can be proposed for cultivars of diverse crop types, including grasses, herbs and tuberous plants. Even though archaeobotanical, biological, ecological and genetic information is often fragmentary, these phenotypic commonalities can be tentatively compared to the domestication syndrome in sexually-reproduced crops (Table 2). Syndrome traits comprise those associated with early domestication common to all derived varieties rather than improvement/diversification traits to have arisen in only some regional varieties (Purugganan and Fuller 2009; Meyer and Purugganan 2013). None of these traits is ubiquitous, with convergence and divergence exhibited for several traits among vegetatively-propagated crops (McKey et al. 2010; Meyer et al. 2012).

Mode of reproduction

Asexual reproduction can develop in plants in numerous ways, some natural and some anthropic, and become dominant in cultivars through: a shift from sexual to asexual reproduction leading to sexual dysfunction and potential loss of sex; spontaneous mutation to create, with subsequent selection of, parthenocarpic forms; preferential selection for seed-suppressed and seedless forms; and, hybrid dysfunction and polyploidisation. Although the reduced ability for sexual reproduction is convergent in many vegetatively-propagated crops, it is achieved through different phenotypic changes and different types of human-plant domesticatory practice. The loss of sexual reproductive capacity has been accompanied by a shift towards perennial life-cycles.

As people have focussed upon the vegetative mode of reproduction, some cultivated plants partially or completely lost their capacity to reproduce sexually through the accumulation of genetic characteristics (e.g., asynchronous flowering, somatic mutations, seed suppression and polyploidy) that would naturally be deleterious to the plant. Similar loss of sex has been noted for plants in environments marginal for viable sexual reproduction (Eckert 2002; Barrett 2015). Prolonged clonal reproduction potentially led to the loss of sexual reproductive capacity for greater yam (*Dioscorea alata;* Alexander and Coursey 1969) and Ethiopian domesticated enset (*Ensete ventricosum*; Hildebrand 2003; Borrell et al. 2019). By contrast, many other crops have maintained sexual reproductive capacity despite prolonged asexual cultivation, such as manioc and sweet potato.

Parthenocarpy is a spontaneous mutation that enables plants to produce mature fruits without fertilisation. The resultant fruits can contain embryonic, immature, or impartially formed seeds that are often more digestible. Parthenocarpy enables plants to be moved beyond the natural range to new environments in which they are unable to sexually reproduce, perhaps due to unfavourable climate, an absence of pollinators, or an absence of sexual partners.

Although plants can then be subject to asexual reproduction, some may still reproduce sexually if fertilised, as occurs in figs (*Ficus carica*; Condit 1947). Of relevance here, anthropic selection of parthenocarpic forms of diploid banana (*Musa* cvs.) in the Southeast Asia-New Guinea region was fundamental to the domestication of major cultivar groups during the mid-Holocene (Perrier et al. 2011). Subsequent human selection during cultivation led to the creation of seed-suppressed and eventually seedless forms in parthenocarpic plants, e.g., vestigial seeds in most banana cultivars (*Musa* cvs.) today.

Hybrid dysfunction leading to sterility is a possible factor underlying vegetative domestication. Introgression, or hybridisation, can lead to sterility and necessitate asexual modes of reproduction in a plant. Sterile hybrid cultivars with odd sets of chromosomes were also generated through polyploidisation and subsequently propagated by people, including triploid bananas (*Musa* cvs.; Perrier et al. 2011), polyploid cane grasses (*Saccharum* spp.; Premachandran et al. 2011) and, arguably, some yams (*Dioscorea* spp.; Lebot 2009). Cultivated polyploids likely developed spontaneously, such as when cultivated banana diploids were brought together or into contact with other cultivated or wild diploids (Perrier et al. 2011).

The idea of polyploidy being a domestication trait is uncertain. Although 78% of perennial crop plants, of which 90% were primarily vegetatively-propagated, were claimed to exhibit ploidy changes as a domestication trait (Ramsey and Schemske 2002), the proportion of polyploids among crops is not statistically different from that among wild species of the same families (Meyer et al. 2012). Rather than being a product of domestication, polyploidy is a natural phenomenon that drives speciation in plants, conferring greater flexibility with the appearance of novel traits (Alix et al. 2017; Smýkal et al. 2018). Humans have benefited from this phenomenon and selected polyploid variants due to useful agronomic traits;

triploids are associated with greater disease resistance and wider environmental tolerances than diploids.

The domestication histories for some crop plants that are predominantly vegetatively-propagated today include episodes of sexual reproduction in the past, including cultigens and some derived from a wild conspecific ancestor, such as the greater yam (*D. alata*; Lebot et al. 1998). Such overlaps between sexual and asexual modes of reproduction continue to the present; several vegetatively-propagated species undergo spontaneous sexual reproduction with wild (where present) or cultivated populations. The resultant progeny are then incorporated into a cultivator's vegetatively-propagated stock to increase cultivar diversity, as documented for manioc (*M. esculenta*; Rival and McKey 2008; Clement et al. 2010), sweet potato (*I. batatas*; Yen 1974) and yams (*Dioscorea* spp.; Dumont and Vernier 2000), as well as for diploid banana (*Musa* cvs.) and taro (*C. esculenta*) cultivars (Kennedy and Clarke 2004). As McKey et al. (2010) observed, cultivated stock of many vegetative crops reflect clonal and some spontaneous sexual reproduction with differing selective pressures that produce complex domestication pathways.

On the whole, vegetatively-propagated cultivars tend to lose sexual reproductive capacity with a concomitant increase in phenotypic characteristics associated with asexual reproduction. Cultivars tend towards parthenocarpy, seed-suppression, and triploid/polyploid sterility. However, these are tendencies rather than inevitable transformations.

Yield of the edible portion

As in sexually reproduced plants, the yield of the edible portion – often the size, but also the availability of useful nutrients – has increased. The increase can be observed in many

underground storage organs (USOs), the fruits of bananas and plantains, and the sugar-enriched stems of some cane grasses. For instance, starch content and storage root yield have been selected for in manioc (Wang et al. 2014), with similar claimed genetic selection in potatoes (Hardigan et al. 2017) and some yams (Scarcelli et al. 2019). Often, the increased size of the edible plant part derives from structures used for vegetative propagation, such as in most USOs (Table 3) including yam tubers (*Dioscorea* spp.; Zannou et al. 2006) and taro corms (*C. esculenta*; Matthews et al. 2012), as well as stems of cane grasses (*S. officinarum*; James 2004). In other plants these characteristics do not align: increased fruit size in banana cultivars cultivated from suckers and increased tuber size in sweet potatoes reproduced from vine slips.

Domestication has also favoured plants with greater in-ground storage capacity. Yams (*Dioscorea* spp.) are an important resource across the tropics due to lengthy tuber dormancy (2-4 months at ambient temperature) facilitating storage for 4-6 months without significant deterioration of nutritional properties (Lebot 2009). Similarly, piecemeal harvesting of USOs can occur over extended periods, such as up to 9 months in sweet potato (Lebot 2009).

Increased yield is also facilitated by increasing the number of edible parts within a plant and through increasing the ratio of edible to non-edible parts. These can be affected in numerous ways: from increasing the quantity of extractable sugar within cane grass stems, to increasing the number and size of fruits and USOs on a plant. Some of these changes are likely the result, at least initially, of phenotypic plasticity, as has been identified for traditional cultivation practices of African wild yams (*Dioscorea* spp.), where putative 'fixation' of newly desired traits may take between 3-5 years (Zannou et al. 2006), while relaxation of cultivation practices results in yams returning to the wild phenotype (Dumont and Vernier 2000).

In some vegetatively-propagated plants, a reduction in seed size (seed suppression) occurs – such as bananas (*Musa* cvs.) – with a concomitant increase in size of the edible fleshy part of the fruit. However, seed suppression has been noted in some sexually-reproduced crops, such as some varieties of cultivated citrus fruits (Roose et al. 1995) and chempedak (*Artocarpus integer*; Primack 1985). In other edible fruits, increased seed size occurred with domestication, even if later suppression of seeds became possible with vegetative reproduction, for example in grapes (*Vitis vinifera*) and *Citrus* spp. In some sexually-reproduced crops that are grown for roots and not seeds, such as carrot (*Daucus carota*) and burdock (*Arctium lappa*), there is also a noted increase in seed size (Kluyver et al. 2017). Hence, the correlation between seed-size and domestication is not ubiquitous, rather it appears correlated with sexual proclivity.

Despite selection under cultivation for millennia, the degrees to which tuber size and starch contents reflect genetic control or conditions of growth are unclear. Morphological changes in plant and tuber morphology have been noted for numerous root crops, such as size and shape in yams (*Dioscorea* spp.; Lea 1966; Hather 2000). They depend upon growth environment and cultivation practices, including degree of soil preparation in garden plots, staking of vines, spacing between plants and weeding. For instance, failure to adequately prepare and maintain cultivated yam plots, especially to enable sufficient leaf area, leads to reduced yields and cultivars rapidly deteriorate, losing beneficial traits and becoming 'feral' (Vernier et al. 2003). Phenotypic variability and likely gene flow between wild and cultivated yams often makes definition of domesticate, feral and wild populations extremely difficult (Scarcelli et al. 2006; cf. Scarcelli et al. 2019).

Ease of harvesting

The developments of fused, multiple or aggregate syncarps, as well as bunching, may have evolved in response to human-mediated domestication, as well as plausibly to enhance seed dispersal by other animals. These morphological changes are demonstrated by a range of fruit and nut-bearing species, including bananas (*Musa* cvs.), as well as berries (*Rubus* spp.), breadfruit (*A. altilis*), figs (*Ficus carica*) and pandanus (*Pandanus* spp.). By contrast, there is a tendency for greater separation amongst USOs, such as potatoes (*S. tuberosum*), sweet potatoes (*I. batatas*) and yams (*Dioscorea* spp.), especially in more friable, cultivated soils, which are plausibly plastic responses to growth environment as much as the product of genetic change. The contrasting fusion of fruit/nuts versus separation in USOs likely results from practices of human harvesting, selection and cultivation, as well as responses to growth environment.

Timing of production

Asynchronous production in vegetatively-propagated crops is a function of two factors: climate and human selection. Today vegetative forms of cultivation predominate as forms of subsistence agriculture in wet tropical and subtropical regions, principally where climates are perhumid and less seasonal. On the whole, vegetative forms of agriculture, or vegeculture, are anticipated to be less seasonal and to enable cultivation of crops at different times of the year. There are notable exceptions: some vegetative crops are major staples in highly seasonal climates, such as potatoes (*S. tuberosum*) in northern Europe and sweet potato (*I. batatas*) on the North Island of New Zealand, although neither plant originates in those regions. For some plants, aseasonal climates lead to less predictable fruit production, in terms of inter-plant synchronicity of production and periodicity of fruit production by individual plants (Bourke et al. 2004). Overall, vegetative crop plants display considerable variation:

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cultivated yams (*Dioscorea* spp.) are persistently photoperiod sensitive despite extensive breeding programs (Lebot 2009). While domesticated seed crops are characterized by more even ripening and narrowing of the harvest window (Ladizinsky 1998; Fuller 2007), human selection seems to have pushed for a broadening harvest window for many vegetative domesticates.

Plant architecture

Apical dominance is manifest in several vegetatively-propagated crops, including potato (*S. tuberosum*), sugarcane (*S. officinarum*), taro (*C. esculenta*) and yams (*Dioscorea* spp.). Apical dominance is well-known in seed crops, often involving selection for taller, erect plants and fewer side branches, or more compact plants, as it allows more plants to fit into each unit of cultivated soil (Doust 2007). In vegetatively propagated crops, there is much variation: yams have been characterised as exhibiting apical dominance (Coursey 1967; Passam 1977), while others propose basal dominance (Mozie 1984); in manioc (*M. esculenta*), apical dominance becomes more marked with reduced spacing between plants (Streck et al. 2017); and, among cultivated bananas triploid AAB plantains (*Musa* cvs.) exhibit more marked apical dominance than diploids and AAA triploids (Ortiz and Vuylsteke 1994). However, some crops exhibit considerable morphological plasticity reflecting growth environment; for instance, wild and cultivated manioc (*M. esculenta*) grows as a liana in forest and dense vegetation, yet as a shrub in open savanna and gardens (Ménard et al. 2013). Apical dominance can be reduced through removal of the shoot tip or sucker in most crops, leading to plural lateral bud development.

Apical dominance is also expressed in terminal flower and seed head/pod character. Although ordinarily associated with sexually reproduced crops, such as soybean (*Glycine max*) and cereal panicles that become larger and concentrated on fewer stalks (Doust 2007; Fuller 2007), comparable morphological transformations may have occurred in some vegetatively propagated crops. For example, lowland *pitpit* (*S. edule*) is a cane grass that is cultivated from cuttings for its unopened flower heads that are cooked as a vegetable in lowland New Guinea (French 2006).

Defensive adaptations

The loss of defensive adaptations, such as spines and armatures in some cultivars may be indications of domestication, as exhibited by several cultivated aroids (*Alocasia macrorrhizos, Amorphophallus paeoniifolius, Cyrtosperma merkusii*; Brown 2000) and many yams (Mignouna and Dansi 2003; Vernier et al. 2003). For example, giant swamp taro (*C. merkusii*) is cultivated from Peninsular Malaysia across the Micronesian atolls to far eastern Polynesia (Hay 1988: 433). Normally the plant is heavily armatured, but under cultivation is usually without armatures and larger in size. Cultivated varieties of elephant foot yam (*A. paeoniifolius*) are also have smoother stalks, as well as fewer raphides and lower-to-no alkaloid content (Brown 2000).

Many crops have been selected for reduced acridity, bitterness, irritability and toxicity to thereby decrease processing requirements and increase palatability, such as lower glycoalkaloids in potatoes (*S. tuberosum*), lower calcium oxalate crystals in taro (*C. esculenta*) and lower dioscorine in yams (*Dioscorea* spp.). One primary secondary metabolite that may impact negatively on human health are cyanogenic glucosides that are hydrolysed

by β-glycosidases into hydrocyanic acid (HCN). A single dose of 1-3 mg/kg of body weight is lethal to most vertebrates (Oke 1969). The presence of cyanogenic glucosides is a heritable trait that may be present in all individuals of some species, while others are heterogenous and may contain acyanogenic individuals (Gleadow and Møller 2014: 163). Cyanogenic glucosides occur in higher concentrations in young plants and production appears to be influenced partially by genetic control (Wang et al. 2014) and partially by local environmental factors such as herbivory, the presence of toxins in soil, reduced soil nutrients, drought and shade (Gleadow and Møller 2014: 170). Depending upon the degree of plasticity inherent in the plant, the act of bringing young plants into a cultivated plot with better soil, sunshine and water, may be enough to significantly reduce the production of cyanogenic glucosides. Under drought stress, manioc (*M. esculenta*) tubers increase in toxicity, sometimes to hazardous concentrations, but this can be reversed by watering (Gleadow and Møller 2014: 171). Pathways to domestication may involve selection of plants with appropriate phenotypic properties, including concentrations of phytochemicals, but also may involve harnessing the plasticity of plants under cultivation through changes in local environmental conditions and the removal of conditions that stress young plants in their early growth phase.

A focus on less acrid, bitter and toxic varieties is not ubiquitous. In manioc (*M. esculenta*), cultivars are grouped into two main types, sweet and bitter, based on respective higher and lower cyanogenic glucoside contents. Bitter manioc requires leaching, mashing and heating to remove toxins, whereas sweet manioc requires only standard cooking and some varieties can be eaten raw (Rival and McKey 2008). Early cultivation may have selected for reduced toxicity in manioc, with highly toxic forms selected later for higher productivity on poor soils and greater storability, even though they require advanced detoxification methods (Arroyo-

Kalin 2012). Similarly, some yams have retained bitterness or toxicity and are still highly poisonous to people, such as the Asiatic bitter yam (*D. hispida*) despite prolonged exploitation for c. 20,000 years (Barton and Paz 2007).

While selection for removal of phytochemicals, usually secondary metabolites, is desirable in plants targeted for general consumption, it seems equally plausible that there has been selection towards greater levels of toxicity in some species, as with bitter manioc (*M. esculenta*). The persistence of bitterness and toxicity in some crops may have reduced competition from mammals, such as pigs and deer, as well as loss to pests, such as beetles and other insects during cultivation and storage. Thus definitions of domestication traits in plants are more complicated than assuming the direction of selection is solely towards a reduction in phytochemicals through time; rather they require consideration of the various stages of food supply – including propagation, cultivation, harvesting, storage, distribution, processing and cooking - and the total range of plant uses, including medicines, toxins, mastics and fibres, as well as food.

Pre- and post-domestication traits

Some characteristics often assumed to derive from domestication are associated with predomestication and postdomestication processes. For instance, ease of storage is potentially a factor that led people to initially target a given species, together with its culinary and nutritional benefits. Several other characteristics are best considered as secondary domestication traits associated with varietal diversification (Purugganan and Fuller 2009; Meyer and Purugganan 2013). Foremost, the vast phenotypic variation exhibited in most root crops, comprising several hundred cultivars in banana, manioc, potato, taro and sweet potato,

among many others, result from centuries and millennia of cultivation. Environmental tolerance, photoperiod sensitivity and disease resistance likely also result from later cultivation practices. Selection of tolerant and resistant phenotypes would presumably be based on cultivator experience, namely, seeing which varieties grow best in specific environments. As varieties were moved into new environments, different phenotypes with different characteristics were preferred. Triploids generally have greater environmental tolerance compared to diploids of the same crop because of the broader genetic inheritance of the former. However, clonally-reproduced, sterile triploids can be highly susceptible to pathogens given the narrow genetic base of cultivated stock, as witnessed with the decimation of global Gros Michel banana plantations by a strain of Panama disease (*Fusarium oxysporum*) in the early 1950s. Further, several traits associated with consumption, processing and cooking of a crop have been refined as secondary domestication traits, including shape, colour, texture and taste.

A domestication syndrome?

While subject to prolonged and continued cultivation, vegetatively-propagated field crops exhibit several domestication traits that are broadly convergent across a range of different groups of plants, including grasses, root crops and vegetables. None of these domestication traits is ubiquitous and there is considerable divergence among crops for some traits. Although a domestication syndrome of convergent traits is proposed for vegetatively-propagated crops here, this is only preliminary.

Significant focus on the genetic aspects of domestication has contributed to our understanding of the mechanisms and origins of many domesticates and key domestication

traits. However, phenotypes of clonal plants are not just genetically controlled; they may display various degrees of 'plasticity' resulting from environmental influences (de Kroon et al. 1994: 125-126). Plasticity is defined as phenotypic change that is environmentally induced, though the direction and the magnitude of that change is genetically determined. There appears to be considerable variation among clonal plants in the degree to which observed phenotypic change may be considered plastic or non-plastic (i.e. that which is under direct genetic control) in different ecological conditions (Ding and Chen 2018; Liu et al. 2019). More 'fixed' morphogenetic changes include a shift towards asexual modes of reproduction and increased edible portion in some plants. Other traits seem to be more plastic, such as yield, ease of harvesting, timing of fruit production, some aspects of plant architecture and some defensive adaptations; consequently, phenotypes readily revert to 'wild type' when left to grow feral.

The archaeobotany of domestication under vegetative propagation

Three advances in archaeobotany have aided the investigation of early agriculture and plant domestication based on vegetative reproduction: phytoliths (Piperno 2006); starch granules (Torrence and Barton 2006), sometimes supplemented with raphide identification (Loy 2006); and, archaeological parenchyma (Hather 2000) (Figures 3-4). Ordinarily, these microfossil techniques are only able to reliably discriminate to genus or family level; higher resolution inferences of species, subspecies and domestication status are often problematic. The application of this suite of techniques has raised the visibility of early plant exploitation and cultivation practices based on vegetative propagation in the lowland neotropics (Piperno and Pearsall 1998), New Guinea region (Denham et al. 2003; Golson et al. 2017), and West African rainforest (Mbida et al. 2001). For instance, at Kuk Swamp in the highlands of Papua

New Guinea, microfossils from stratigraphic contexts and as residues on stone artefacts provide evidence for the presence and use of various plants, respectively (Golson et al. 2017). However, interpretations of early cultivation, as a surrogate measure for the intensity of domesticatory relationships, have relied upon the association of archaeobotanical remains with multiple lines of contextual evidence, including: archaeological features associated with cultivation, such as field systems, mounds and ditches; palaeosols and feature fills consistent with plot preparation, tillage and cultivation; and, palaeoecological records of forest clearance, weedy and fallow floral assemblages, and burning (Denham 2018).

The initial step in the archaeobotany of vegetative plant domestication is to obtain a species identification, with subsequent discrimination of wild-domesticated morphotypes where possible. Although species-level identification is often achievable for most fruit and nut-bearing species from seeds and nut-fragments, respectively, it has proven problematic for a number of cane grasses, root crops and vegetables (Pearsall 2000). For instance, although many species of aroids have large numbers of calcium oxalate crystals present as druses and raphides in cellular tissues (Brown 2000: 276-277), which may be identifiable to genus level (Crowther 2009a), they are not ordinarily well-preserved in archaeological contexts nor are they ordinarily identified during archaeobotanical investigations (though see Loy et al. 1992); consequently, the identification of taro in the past has been heavily reliant on charred parenchyma and starch granule morphometrics (Fullagar et al. 2006). Nonetheless, the exploitation of several vegetatively-propagated plants has been identified in archaeobotanical contexts using phytoliths and starch granules. Even though microfossils do not ordinarily, nor reliably, discriminate between wild and domesticated types, these remains are often inferred to represent cultivation because they were found outside the natural range (e.g., Piperno and Pearsall 1998; Vrydaghs et al. 2003; Chandler-Ezell et al. 2006).

Macro-remains of preserved fruits, tubers and stem fragments can preserve in desiccated or charred form. Macrobotanical tuber fragments of potato (*S. tuberosum*) have been documented from 10,000 year-old archaeological contexts in the Chilca Canyon, central coast of Peru (Engel 1970). The desiccated macro-remains of achira (*Canna edulis*), manioc, potato and sweet potato were found at multiple sites dating from c. 4250-3500 years ago in the Casma Valley, Peru (Ugent et al. 1981, 1982, 1984, 1986; Ugent and Peterson 1988). Banana (*Musa* sp.) skin peelings, taro (*C. esculenta*) corms and sugarcane (*S. officinarum*) stem sections at the Red Sea port of Quseir al-Qadim in Egypt indicate westward trade in vegetative cultivars to Africa by 1040-1160 AD (Van der Veen and Morales 2011).

Charred parenchyma fragments are more commonly encountered on archaeological sites across the globe, but there have been recurrent problems with obtaining reliable taxonomic identifications (Hather 1988, 1991, 1994a, 1994b, 1996, 2000; Paz 2001; Oliveira 2008; Barton et al. 2016). Fragments of charred sweet potato (*I. batatas*) have been identified from several sites in Hawai'i dating from 1300 AD (Ladefoged et al. 2005) and in eastern Polynesia from 1000-1200 AD (Hather and Kirch 1991), although such robust identifications are rare. Charred sugarcane (*S. officinarum*) stem and sweet potato (*I. batatas*) tuber fragments from recent domestic contexts at Kuk Swamp have been identified using optical microscopy and microCT and are suggestive of continuities with ethnographic lifestyles in the highlands of New Guinea (Lewis et al. 2016; Pritchard et al. 2018).

Even if a species-level identification is possible, the discrimination of domesticates from wild-types is problematic. Problems result from: a limited understanding of plant ecology, phenology and genetics; a lack of clarity in terms of domestication traits; and, uncertainties in the archaeobotanical identification of domestication traits in plant micro and macrofossils. Further, any domestication traits in vegetatively-propagated plants may be difficult to identify

in the archaeobotanical record because the specific traits preserved need not be 'fixed' in the same way as early domestication traits in some sexually-reproduced crops, such as non-shattering spikelet bases. Rather, phenotypic traits in many vegetatively-propagated plants still seem to exhibit considerable developmental plasticity, which makes interpretations of domestication status for archaeobotanical remains from the distant past problematic. The implications of phenotypic plasticity for using archaeobotany to reconstruct the fixation of traits during a domestication episode in the past are unclear. Some aspects of USO macromorphology and plant parenchyma, such as cell wall thicknesses and size, as well as starch granule morphologies and sizes, may be plastic to varying (and largely unknown) degrees thereby confounding the charting of domestication in the archaeobotanical record using these macrofossil and microfossil techniques.

The implications of morphological plasticity at the microscale, namely, in terms of starch granule and phytolith morphometrics, parenchyma cell wall thicknesses and phytochemistry require systematic study for most species, whether in terms of domestication status (Ugent et al. 1982; Perry 2002; Barton et al. 2016; Herzog et al. 2018), or in terms of growth environment (Field 2006). Increases in parenchyma cell size and cell wall thickness have been identified between wild and domesticated varieties of some taro (*C. esculenta*) and some yams (*Dioscorea* spp.; Barton et al. 2016), but the field overall lacks systematic study. By contrast in bananas (*Musa* spp.), volcaniform phytoliths show a c. 20% increase in crater size from AA diploids to cultivated AAA triploids (Ball et al. 2006; Vrydaghs et al. 2009), although this size change is not consistent across all diploid and triploid cultivar groups (De Langhe et al. 2019). Similarly, elevated or reduced levels of acridity, bitterness, toxicity and other irritants in some tuberous plants are associated with domestication, although contents often vary with lifecycle stage (Sunell and Healey 1979, 1985) and growing conditions, e.g.,

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soil nutrients, water stress, shade and herbivore behaviour (Metlen et al. 2009). Potentially, phytochemical contents could be measured in desiccated or charred parenchymatous tissues if suitably preserved, such as calcium oxalate raphides and druses in taro (Figure 4; *C. esculenta*; Crowther 2009b).

Taken together, archaeobotanical evidence for the early domestication of vegetative plants is relatively sparse and often ambiguous. Although phenotypic differences between domesticates and wild precursor(s) are known for many vegetatively-propagated crop plants, the timing for the emergence of domestic traits and the duration of the domestication episode have not been tracked in the archaeobotanical record. In part, archaeobotanical techniques may not always be suitable – as noted above for starch granules, phytoliths and archaeological parenchyma – for differentiating between wild and domestic plants. More significantly, these archaeobotanical techniques have not been systematically applied and comprehensive modern reference collections of wild and domesticated plants have not been developed for most vegetative crops. More fundamentally, the effects of developmental plasticity are poorly understood in terms of how plant microfossils and microfossils of vegetatively-propagated crops present in the archaeobotanical record.

Conclusion

A domestication syndrome of convergent evolutionary traits has been proposed for sexually-reproduced crops that can be tracked in the archaeobotanical record through the emergence of non-shattering cultivars and, to a lesser extent, through increased seed-size (Fuller et al. 2014; 2018). Several domestication syndrome traits in these crops are fixed and have known genetic markers, namely there is some correspondence between phenotype and genotype (Fuller and

Allaby 2009; Meyer and Purugganan 2013). Increasingly, ancient DNA can be used to track directly the emergence of genetic markers of domestication for sexually reproduced plants in the past (Jaenicke-Despres et al. 2013; Castillo et al. 2016; Allaby et al. 2018; Kistler et al. 2018).

Equivalent domestication syndrome traits in vegetatively-propagated crop plants display convergent, as well as some divergent, traits. There are convergent tendencies to lose sexual reproductive capacity and increase the size of the edible portion, although other traits are divergent, and none are ubiquitous. Whereas in sexually reproduced plants phenotypic and genotypic transformations associated with domestication are portrayed as occurring in lockstep, considerable variation exhibited by vegetatively-propagated plants likley represents phenotypic plasticity rather than genotypic variation. Currently, the application of aDNA to the investigation of clonal domestication is limited, partly due to poor biomolecular preservation in charred plant tissues and partly due to the lack of application, especially to desiccated plant remains.

Although the domestication syndrome in sexually reproduced plants may be overstated (Meyer et al. 2012; Abbo et al 2014), phenotypic traits are still characterised as correlated with genotypes resulting from human-directed selection and genetic isolation (Fuller and Allaby 2009; Larson et al. 2014). In this sense, sexual domestication processes represent a Darwinian 'best fit' to human selection and anthropic environments. In vegetatively-propagated plants, plastic adaptation to growth environments fulfils a similar function in terms of driving phenotypic variation. Whilst the effects of plasticity are arguably more evident in the phenotypes of vegetatively-propagated plants, there is still an underlying element of genetic alteration through natural mutation, introgression and other phenomena affecting the genetic code and how it is expressed phenotypically through time.

Many clonal domestication traits in vegetatively-propagated crops result from active and recurrent practical management of the plant and its growth environment by people. Although genetic markers provide the biomolecular scaffolding for any domestication traits, recurrent behavioural practices that manage plants and growth environments influence phenotypic expression. We wonder if the role of cultivation practices in determining the expression of domestication traits has been underestimated in vegetatively-propagated field crops, as well as in some sexually-reproduced crops.

Vegetatively-propagated crops are globally significant to understanding the emergence of agriculture, as well as to planning for more sustainable agricultural futures. Yet the domestication histories for most vegetatively-propagated crops are poorly known. Domestication syndrome traits in vegetative crops represent tendencies in human-mediated plant evolution that reflect a combination of permanent genetic changes and impermanent plastic responses to practices of cultivation, includingplant propagation and managing the conditions of growth, such as vegetation clearance and plot preparation. The respective roles of genetic regulation and phenotypic plasticity in the development and expression of domestication traits are uncertain. Co-ordinated botanical and archaeobotanical research is urgently needed in different parts of the world to further our understanding of how people domesticated plants through various practices of vegetation propagation in the past.

References

Abbo S, van-Oss RP, Gopher A, Saranga Y, Ofner I, Peleg Z. 2014. Plant domestication versus crop evolution: a conceptual framework for cereals and grain legumes. *Trends in Plant Science* 19: 351-360.

Abrahamson WG. 1980. Demography and vegetative reproduction. In: Solberg OT, ed., *Demography and Evolution in Plant Populations*. Oxford: Blackwell Scientific Publications, pp. 89-106.

Alexander J., Coursey DG.1969. The origins of yam cultivation. In: Ucko PJ, Dimbleby GW, eds., *The Domestication and Exploitation of Plants and Animals*. London: Gerald Duckworth, pp. 405–425.

Alix K, Gerard PR, Schwarzacher T, Heslop-Harrison JS. 2017. Polyploidy and interspecific hybridisation: partners for adaptation, speciation and evolution in plants. *Annals of Botany* 120: 183-194.

Allaby RG. 2014. Domestication syndrome in plants. In: Smith C, ed., *Encyclopedia of Global Archaeology*. New York: Springer, pp. 2182–2184.

Allaby RG, Ware RL, Kistler L. 2018. A re-evaluation of the domestication bottleneck from archaeogenomic evidence *Evolutionary Applications* 12: 29-37

Arroyo-Kalin M. 2012. Slash-burn-churn: landscape history and crop cultivation in pre-Columbian Amazonia. *Quarternary International* 249: 4-18.

Ball TB, Vrydaghs L, Van Den Hauwe I, Manwaring J, De Langhe E. 2006. Differentiating banana phytoliths: wild and edible *Musa acuminata* and *Musa balbisiana*. *Journal of Archaeological Science* 33: 1228–1236.

Barrau J. 1955. *Subsistence Agriculture in Melanesia*. Noumea: New Caledonia.

Barrett SC. 2015. Influences of clonality on plant sexual reproduction. *Proceedings of the National Academy of Sciences of the United States of America* 112: 8859-8866.

Barron A, Turner M, Beeching L, *et al.* 2017. MicroCT reveals domesticated rice (*Oryza sativa*) within pottery sherds from early Neolithic sites (4150-3265 cal BP) in Southeast Asia. *Scientific Reports* 7: 7410.

Barton H, Denham TP. 2018. Vegecultures and the social-biological transformations of plants and people. *Quaternary International* 489: 17-25.

Barton H, Paz V. 2007. Subterranean diets in the tropical rainforests of Sarawak, Malaysia. In: Denham TP, Iriarte J, Vrydaghs L, eds., *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*. Walnut Creek, CA: Left Coast Press, pp. 50–77.

Barton H, Paz V, Carlos AJ. 2016. Plant food remains from the Niah Caves: macroscopic and microscopic approaches. In: Barker G, Farr L, eds., *Archaeological Investigations in the Niah Caves, Sarawak*. Vol. 2. Cambridge: McDonald Institute for Archaeological Research, pp. 455-468.

Bitocchi E, Rau D, Bellucci E, *et al.* 2017. Beans (*Phaseolus* ssp.) as a model for understanding crop evolution. *Frontiers in Plant Science* 8: 722.

Borrell JS, Biswas MK, Goodwin M, *et al.* 2019. Enset of Ethiopia: a poorly characterized but resilient starch staple. *Annals of Botany* XX: 1-20.

Bourke RM, Camarotto C, D'Souza EJ, Nema K, Tarepe TN, Woodhouse S. 2004. *Production Patterns of 180 Economic Crops in Papua New Guinea*. Canberra: Coombs Academic Publishing.

Brown D. 2000. *Aroids: Plants of the Arum Family* (2nd Edition). Portland, Oregon: Timber Press.

Bruno M. 2009. Practice and history in the transition to food production. *Current Anthropology* 50: 703–706.

Burkill IH. 1935. *A Dictionary of the Economic Products of the Malay Peninsula. 2 Volumes*. London: Crown Agents.

Castillo CC, Tanaka K, Sato YI, *et al.* 2016. Archaeogenetic study of prehistoric rice remains from Thailand and India: evidence of early japonica in South and Southeast Asia. *Archaeological and Anthropological Sciences* 8: 523-543.

Chaïr H, Traore RE, Duval MF, *et al.* 2016. Genetic diversification and dispersal of taro (*Colocasia esculenta* (L.) Schott). *PLOS ONE* 11(6): e0157712. doi: 10.1371/journal.pone.0157712

Chandler-Ezell K, Pearsall DM, Zeidler JA. 2006. Root and tuber phytoliths and starch grains document manioc (*Manihot esculenta*), arrowroot (*Maranta arundinacea*) and llerén (*Calathea* sp.) at the Real Alto site, Ecuador. *Economic Botany* 60: 103-120.

Chen YH, Ruiz-Arocho J, von Wettberg EJB. 2018 Crop domestication: anthropogenic effects on insect–plant interactions in agroecosystems *Current Opinion in Insect Science* 29: 56-63

Clement CR, de Cristo-Araújo M, d'Eeckenbrugge GC, Pereira AA, Picanço-Rodridgues D. 2010. Origins and domestication of Native American crops. *Diversity* 2: 72–106.

Condit IJ. 1947. *The Fig*. Waltham: Chronica Botanica.

Coursey DG. 1967. *Yams. An Account of the Nature, Origins, Cultivation and Utilisation of the useful members of the Dioscoreaceaa*. London: Longmans.

Crowther A. 2009a. Morphometric analysis of calcium oxalate raphides and assessment of their taxonomic value for archaeological microfossil studies. In: Haslam M, Robertson G, Crowther A, Nugent S, Kirkwood L, eds, *Archaeology under a Microscope: Studies in Residue and Ancient DNA Analysis in Honour of Thomas H. Loy*. Canberra: ANU Press, pp. 102-128.

Crowther A. 2009b. Re-viewing raphides: issues with the identification and interpretation of calcium oxalate crystals in microfossil assemblages. In: Fairbairn AS, O'Connor S, Marwick B, eds., *New Directions in Archaeological Science*. Canberra: ANU Press, pp. 105-118.

D'Andrea A, Kahlheber S, Logan A, Watson D. 2007. Early domesticated cowpea (*Vigna unguiculata*) from Central Ghana. *Antiquity* 81: 686-698.

de Kroon H, Stuefer JF, Dong N, During HJ. 1994. Plant morphology and its ecological significance. *Folia Geobotanica & Phytotaxonomica* 29: 123-138.

De Langhe E, Perrier X, Donohue M, Denham TP. 2015. The original banana split: Multidisciplinary implications of the generation of African and Pacific Plantains in Island Southeast Asia. *Ethnobotany Research and Applications* 14: 299-312.

De Langhe E, Vrydaghs L, Perrier X, Denham TP. 2019. Fahien reconsidered: Pleistocene exploitation of wild bananas and Holocene introduction of Musa cultivars to Sri Lanka. *Journal of Quaternary Science* 34: 405-409.

Denham TP. 2018. *Tracing Early Agriculture in the Highlands of New Guinea: Plot, Mound and Ditch.* Oxford: Routledge.

Denham TP, Iriarte J, Vrydaghs L, eds., 2007. *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives.* Walnut Creek, CA: Left Coast Press.

Denham TP, Haberle SG, Lentfer C, *et al.* 2003. Origins of agriculture at Kuk Swamp in the Highlands of New Guinea. *Science* 301: 189-193.

Ding M, Chen ZJ 2018. Epigenetic perspectives on the evolution and domestication of polyploid plant and crops. *Current Opinion in Plan Biology* 42: 37–48.

Doust AN. 2007. Architectural evolution and its implications for domestication in grasses. *Annals of Botany* 100: 941–950.

Dozy RPA. 1961. *Le Calendrier de Cordoue de L'Année 961: Texte Arabe et Ancienne Traduction Latine accompagnée d'une traduction française annotée par Ch. Pellat.* Leiden: E. J. Brill, 1873.

Dumont R, Vernier P. 2000. Domestication of yams (*Dioscorea cayenensis-rotundata*) within the Bariba ethnic group in Benin. *Outlook on Agriculture* 29: 137–142.

Eckert CG. 2002. The loss of sex in clonal plants. *Evolutionary Ecology* 15: 501–520.

Ellstrand NC. 2003. *Dangerous Liaisons? When Cultivated Plants Mate with their Wild Relatives*. Baltimore: The John Hopkins University Press.

Engel FA. 1970. Explorations of the Chilca Canyon, Peru. *Current Anthropology* 11: 55-58.

FAO (Food and Agriculture Organisation) 2016. *FAOSTAT*. http://www.fao.org/faostat/en Rome: Food and Agriculture Organisation of the United Nations.

Field J. 2006. Reference collections. In: Torrence R, Barton H, eds, *Ancient Starch Research*. Walnut Creek, CA: Left Coast Press, pp. 95-114.

French B. 2006. *Food Plants of Papua New Guinea: A Compendium*. Revised Edition. Burnie, Tasmania: Food Plants International, Inc.

Fullagar R, Field J, Denham TP, Lentfer C. 2006. Early and mid Holocene processing of taro (*Colocasia esculenta*) and yam (*Dioscorea* sp.) at Kuk Swamp in the Highlands of Papua New Guinea. *Journal of Archaeological Science* 33: 595-614.

Fuller DQ. 2007. Contrasting patterns in crop domestication and domestication rates: recent archaeobotanical insights from the Old World. *Annals of Botany* 100: 903-924.

Fuller DQ, Allaby R. 2009. Seed dispersal and crop domestication: shattering, germination and seasonality in evolution under cultivation. In: Østergaard L, ed., *Annual Plant Reviews 38: Fruit Development and Seed Dispersal*. Oxford: Wiley-Blackwell, pp. 238-295.

Fuller DQ, Harvey E. 2006. The archaeobotany of Indian pulses: identification, processing and evidence for cultivation. *Environmental Archaeology* 11: 219-246.

Fuller DQ, Murphy C. 2018. The origins and early dispersal of horsegram (*Macrotyloma uniflorum*), a major crop of ancient India. *Genetic Resources and Crop Evolution* 65: 285-305.

Fuller DQ, Hildebrand EA. 2013. Domesticating plants in Africa. In P. Mitchell and P. Lane (eds) *The Oxford Handbook of African Archaeology*, pp. 507-525. Oxford: Oxford University Press.

Fuller DQ, Denham TP, Arroyo-Kalin M, *et al.* 2014. Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proceedings of the National Academy of Sciences (USA)* 111: 6147-6152.

Fuller DQ, Lucas L, Gonzalez Carretero L, Stevens C. 2018. From intermediate economies to agriculture: trends in wild food use, domestication and cultivation among early villages in Southwest Asia. *Paléorient* 44: 61-76.

Fuller DQ, Murphy C, Kingwell-Banham E, Castillo CC, Naik S. 2019. *Cajanus cajan* origins and domestication: the South and Southeast Asian archaeobotanical evidence. *Genetic Resources and Crop Evolution*. DOI: 10.1007/s10722-019-00774-w

Fuller DQ, Qin L, Zheng Y, Zhao Z, Chen X, Hosoya LA, Sun GP. 2009. The domestication process and domestication rate in rice: Spikelet bases from the Lower Yangtze. *Science* 323: 1607–1610.

Gepts P. 2004. Crop domestication as a long-term selection experiment. *Plant Breeding Reviews* 24: 1–44.

Gleadow RM, Møller BL. 2014. Cyanogenic glycosides: synthesis, physiology, and phenotypic plasticity. *Annual Review of Plant Biology* 65: 155-185.

Golson J, Denham TP, Hughes PJ, Swadling P, Muke J (eds.) 2017. *Ten Thousand Years of Cultivation at Kuk Swamp in the Highlands of Papua New Guinea.* Terra Australis 46. Canberra: ANU E Press.

Grimaldi I, Muthukumuran S, Tozzi G, *et al.* 2018. Literary evidence for taro in the ancient Mediterranean: A chronology of names and uses in a multilingual world. *PLOSONE* https://doi.org/10.1371/journal.pone.0198333.

Grivet L, Daniels C, Glaszman JC, D'Hont A. 2004. A review of recent molecular genetics evidence for sugarcane evolution and domestication. *Ethnobotany Research and Applications* 2: 9–17.

Guedes, JAD'A, Lu H, Heinc AM, Schmidt AH 2015. Early evidence for the use of wheat and barley as staple crops on the margins of the Tibetan Plateau *Proceedings of the National Academy of Sciences (USA)* 115: 5625-5630.

Hammer K. 1984. Das Domestikationssyndrom, *Kulturpflanze* 32: 11-34

Hardigan MA, Laimbeer FPE, Newton L, *et al.* 2017. Genome diversity of tuber-bearing Solanum uncovers complex evolutionary history and targets of domestication in the cultivated potato *Proceedings of the National Academy of Sciences (USA)* 114: E9999-E10008.

Harlan JR. 1971. Agricultural origins: centers and non-centers. *Science* 174: 468-474.

Harlan JR, De Wet JMJ, Price EG. 1973. Comparative evolution of cereals. *Evolution* 27: 311-325.

Harris DR. 1972. The origins of agriculture in the tropics. *American Scientist* 60: 180–193.

Harris DR. 1977. Alternative pathways toward agriculture. *Origins of agriculture*. In: Reed C, ed., *Origins of Agriculture*. The Hague: Mouton, pp. 179-243.

Harris DR. 2002. The expansion capacity of early agricultural systems: a comparative perspective on the spread of agriculture. In: Bellwood P, Renfrew C, eds., *Examining the Farming/Language Dispersal Hypothesis*. Cambridge: McDonald Institute for Archaeological Research, pp. 31–40.

Harris DR. 2007. Agriculture, cultivation and domestication: exploring the conceptual framework of early food production. In: Denham TP, Iriarte J, Vrydaghs L, eds., *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*. Walnut Creek: Left Coast Press, pp. 16–35.

Harper JL. 1977. *Population Biology of Plants*. London: Academic Press.

Hather JG. 1988. *The morphological and anatomical interpretation and identification of charred vegetative parenchymatous plant remains*. Unpublished PhD thesis, University College London.

Hather JG. 1991. The identification of charred archaeological remains of vegetative parenchymatous tissue. *Journal of Archaeological Science* 18: 661-675.

Hather JG. 1994a. A morphological classification of roots and tubers and its bearing on the origins of agriculture in Southwest Asia and Europe. *Journal of Archaeological Science* 21: 719-724.

Hather JG. 1994b. The identification of charred root and tuber crops from archaeological sites in the Pacific, In: Hather JG, ed., *Tropical Archaeobotany: Applications and New Developments*. London: Routledge, pp. 51-64.

Hather JG. 1996. The origins of tropical vegeculture: Zingiberaceae, Araceae and Dioscoreaceae in Southeast Asia. In: Harris DR, ed., *The Origins and Spread of Agriculture and Pastoralism in Eurasia*. London: University College London Press, pp. 538-550.

Hather JG. 2000. *Archaeological Parenchyma*. London: Archaeotype Publications.

Hather JG, Kirch PV. 1991. Prehistoric sweet potato (*Ipomoea batatas*) from Mangaia Island, Central Polynesia. *Antiquity* 65: 887-893.

Hay A. 1988. Cyrtosperma (*Araceae*) and its Old World allies. *Blumea* 33:427–469.

Herzog NM, Louderback LA, Pavlik BM. 2018. Effects of cultivation on tuber and starch granule morphometrics of *Solanum jamesii* and implications for interpretation of the archaeological record. *Journal of Archaeological Science* 98: 1-6.

Hildebrand EA. 2003. *Enset, yams and honey: ethnoarchaeological approaches to the origins of horticulture in southwest Ethiopia*. Unpublished PhD thesis, Washington University in St Louis.

Hildebrand EA. 2007. A tale of two tuber crops: how attributes of enset and yams may have shaped prehistoric human – plant interactions in southwest Ethiopia. In: Denham TP, Iriarte J, Vrydaghs L, eds., *Rethinking Agriculture: Archaeological and Ethnoarchaeological Perspectives*. Walnut Creek: Left Coast Press, pp. 273–298.

Hunt HV, Shang X, Jones MK. 2018. Buckwheat: a crop from outside the major Chinese domestication centres? A review of the archaeobotanical, palynological and genetic evidence. *Vegetation History and Archaeobotany* 27: 493-506.

Isendahl C. 2012. The domestication and early spread of manioc (*Manihot esculenta* Crantz): a brief synthesis. *Latin American Antiquity* 22: 452-468.

Jaenicke-Despres V, Buckler ES, Smith BD, *et al.* 2003. Early allelic selection in maize as revealed by ancient DNA. *Science* 302: 1206-1208.

James G. 2004. An introduction to sugarcane. In: James G, ed., *Sugarcane.* 2nd Edition. Oxford: Blackwell.

Kennedy J, Clarke WC. 2004. *Cultivated Landscapes of the Southwest Pacific*. Resource Management in the Asia-Pacific (RMAP) Working Paper 50, Canberra: RMAP, Australian National University

Kistler L, Maezumi SY, Gregorio de Souza J, *et al.* 2018. Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. *Science* 362: 1309-1313.

Kluyver TA, Jones G, Pujol B, *et al.* 2017. Unconscious selection drove seed enlargement in vegetable crops. *Evolution Letters* 1: 64-72.

Ladefoged TN, Graves MW, Coil JH. 2005. The introduction of sweet potato in Polynesia: early farmers in Hawai'i. *The Journal of the Polynesian Society* 114: 359-373.

Ladizinsky, G. 1985. Founder effect in crop-plant evolution. *Economic Botany* 39: 191-199.

Ladizinsky G. 1998. *Plant Evolution under Domestication*. London: Kluwer Academic.

Larson G, Piperno DR, Allaby RG, et al. 2014. Current perspectives and the future of domestication studies. *Proceedings of the National Academy of Sciences (USA)* 111: 6139-6146.

Lea DAM. 1966. Yam growing in the Maprik area. *Papua New Guinea Agricultural Journal* 18: 5–16.

Lebot V. 2009. *Root and Tuber Crops: Cassava, Sweet Potato, Yams and Aroids.* Crop Production Science in Horticulture, Volume 17. Wallingford: CABI Publishing.

Lebot V, Trilles B, Noyer JL, Modesto J. 1998. Genetic relationships between *Dioscorea alata* L. cultivars. *Genetic Resources and Crop Evolution* 45: 499–509.

Lee GA, Crawford G, Liu L, Sasaki Y, Chen X. 2011. Archaeological Soybean (*Glycine max*) in East Asia: Does Size Matter? *PLOS ONE*
https://doi.org/10.1371/journal.pone.0026720

Lenser C, Theiβen G. 2013 Molecular mechanisms involved in convergent crop domestication *Trends in Plant Science* 18: 704-714.

Lewis T, Denham TP, Golson J. 2016. A renewed archaeological and archaeobotanical assessment of house sites at Kuk Swamp in the highlands of Papua New Guinea. *Archaeology in Oceania* 51(S1): 91-103.

Li H-L. 1970. The origin of cultivated plants in Southeast Asia. Economic Botany 24: 3–19.

Liu W, Chen L, Zhang S, *et al.* 2019. Decrease of gene expression diversity during domestication of animals and plants. *BMC Evolutionary Biology* 19: 19.

Loy TH. 2006. Raphides. In: Torrence R, Barton H, eds., *Ancient Starch Research*. Walnut Creek, CA: Left Coast Press, p. 136.

Loy TH, Spriggs M, Wickler S. 1992. Direct evidence for human use of plants 28,000 years ago: starch residues on stone artefacts from the northern Solomon Islands. *Antiquity* 66: 898-912.

Martinez-Ainsworth NE, Tenaillon ML. 2016. Superheroes and masterminds of plant domestication. *Comptes Rendus Biologies* 339: 268-273.

Matthews PJ, Agoo EMG, Tandang DN, Madulid DA. 2012. Ethnobotany and ecology of wild taro (*Colocasia esculenta*) in the Philippines: Implications for domestication and dispersal. In: Spriggs M, Addison D, Matthews PJ, eds., *Irrigated Taro (Colocasia esculenta) in the Indo-Pacific: Biological, Social and Historical Perspectives*. Osaka: National Museum of Osaka, Senri Ethnological Studies 78, pp. 307-340.

Mbida Mindzie, C, Doutrelepont H, Vrydaghs L, *et al.* 2001. First archaeological evidence of banana cultivation in central Africa during the third millennium before present. *Vegetation History and Archaeobotany* 10: 1–6.

McKey D, Elias M, Pujol B, Duputié A. 2010. The evolutionary ecology of clonally propagated domesticated plants. *New Phytologist* 186: 318–332.

McKey D, Elias M, Pujol B, Duputié A. 2012. Ecological approaches to crop domestication. In: Gepts, P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, Qualset CO, eds., *Biodiversity in Agriculture: Domestication, Evolution and Sustainability*. New York: Cambridge University Press, pp. 377–406.

Ménard L, McKey D, Muhlen GS, Vlair B, Rowe NP. 2013. The evolutionary fate of phenotypic plasticity and functional traits under domestication in manioc: changes in stem

biomechanics and the appearance of stem brittleness. *PLOS ONE* 8(9): e74727.

https://doi.org/10.1371/journal.pone.0074727

Metlen KL, Aschehoug ET, Callaway RM. 2009. Plant behavioural ecology: dynamic

plasticity in secondary metabolites. *Plant, Cell and Environment* 32: 641-653.

Meyer RS, Purugganan MD. 2013. Evolution of crop species: genetics of domestication and

diversification. *Nature Reviews Genetics* 14: 840-852.

Meyer RS, DuVal AE, Jensen HR. 2012. Patterns and processes in crop domestication: an

historical review and quantitative analysis of 203 global food crops. *New Phytologist* 196: 29-

48.

Mignouna HD, Dansi A. 2003. Yam (*Dioscorea* spp.) domestication by the Nago and Fon

ethnic groups in Benin. *Genetic Resources and Crop Evolution* 50: 519–528.

Mock, KE, Rowe CA, Hooten MB, Dewoody J, Hipkins VD. 2008. Clonal dynamics in

western North American aspen (*Populus termuloides*). *Molecular Ecology* 17: 4827-4844.

Mozie O. 1984. The nature of shoot dominance in white yam tubers *Dioscorea rotundata*.

Journal of Agriculture of the University of Puerto Rico 68: 335-340.

Muñoz-Rodríguez P, Carruthers T, Wood JRI, *et al.* 2018. Reconciling conflicting

phylogenies in the origin of sweet potato and dispersal to Polynesia. *Current Biology* 28:

1246-1256.

Murphy CA, Fuller DQ. 2017. The agriculture of early India. In: Shugart H, ed, *Oxford*

Research Encyclopedia of Environmental Science. Oxford: Oxford University Press. Online:

DOI: 10.1093/acrefore/9780199389414.013.169

Oke OL. 1969. The role of hydrocyanic acid in nutrition. *World Review of Nutrition and Dietetics* 11: 170–98

Oliveira N. 2008. *Subsistence archaeobotany: food production and the agricultural transition in East Timor.* Unpublished PhD thesis, Australian National University.

Olsen KM, Schaal BA. 2006. DNA sequence data and inference on cassava's origin of domestication. In: Zeder MA, Bradley DG, Emshwiller E, Smith BD, eds., *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley: University of California Press, pp. 123-133.

Ortiz R, Vuylsteke D. 1994. Genetic analysis of apical dominance and improvement of suckering behavior in plantain. *Journal of the American Society of Horticultural Science* 119: 1050-1053.

Passam HC. 1977. Sprouting and apical dominance of yam tubers. *Tropical Science* 19: 29-39.

Paz V. 2001. *Archaeobotany and cultural transformation: patterns of early plant utilisation in northern Wallacea.* Unpublished PhD thesis, University of Cambridge.

Pearsall DM. 2000. *Paleoethnobotany: A Handbook of Procedures*. 2nd ed. London: Academic Press.

Perrier X, De Langhe E, Donohue M, *et al.* 2011. Multidisciplinary perspectives on banana (*Musa* spp.) domestication. *Proceedings of the National Academy of Sciences (USA)* 108: 11311-11318.

Perry L. 2002. Starch granule size and the domestication of manioc (*Manihot esculenta*) and sweet potato (*Ipomoea batatas*). *Economic Botany* 56: 335-349.

Pickersgill B. 2018. Parallel vs. convergent evolution in domestication and diversification of crops in the Americas. *Frontiers in Ecology and Evolution* 6: 56.

Piperno DR. 2006. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists*. Lanham: AltaMira.

Piperno DR, Pearsall DM. 1998. *The Origins of Agriculture in the Lowland Neotropics*. San Diego: Academic Press.

Premachandran MN, Prathima PT, Lekshmi M. 2011. Sugarcane and polyploidy. *Journal of Sugarcane Research* 1: 1-15.

Primack RB. 1985. Comparative studies of fruits in wild and cultivated trees of chempedak (*Artocarpus integer*) and terap (*Artocarpus odoratissimus*) in Sarawak, East Malaysia with additional information on the reproductive biology of the Moraceae in Southeast Asia. *Malayan Nature Journal* 39: 1-39.

Pritchard J, Lewis T, Beeching L, Denham TP. 2018. An assessment of microCT technology for the investigation of charred archaeological parenchyma from house sites at Kuk Swamp, Papua New Guinea. *Journal of Anthropological and Archaeological Sciences* https://doi.org/10.1007/s12520-018-0648-0

Purugganan MD, Fuller DQ. 2009. The nature of selection during plant domestication. *Nature* 457: 843-848.

Rendón-Anaya M, Montero-Vargas JM, Saburido-Álvarez S, *et al.* 2017. Genomic history of the origin and domestication of common bean unveils its closest sister species. *Genome Biology* 18(1): 60.

Rival L, McKey D. 2008. Domestication and diversity in manioc (*Manihot esculenta* Crantz ssp. *esculenta*, Euphorbiaceae). *Current Anthropology* 49: 1119-1128.

Roose ML, Soost RK, Cameron JW. 1995. Citrus. In: Smartt J, Simmonds NW, eds., *Evolution of Crop Plants*, Second Edition. Harlow: Longman, pp. 443-448.

Roullier C, Benoit L, McKey DB, Lebot V. 2013. Historical collections reveal patterns of diffusion of sweet potato in Oceania obscured by modern plant movements and recombination. *Proceedings of the National Academy of Sciences (USA)* 110: 2205–2210.

Ruddle K, Johnson D, Townsend P, Rees J. 1978. *Palm Sago: a Tropical Starch from Marginal Lands*. Canberra: Australian National University Press.

Santosa E, Lian CL, Sugiyama N, Misra RS, Boonkorkaew P, Thanomchit K. 2017. Population structure of elephant foot yams (*Amorphophallus paeoniifolius* (Dennst.) Nicolson) in Asia. *PLOS ONE* 12(6): e0180000 https://doi.org/10.1371/journal.pone.0180000

Sauer CO. 1952. *Agricultural Origins and their Dispersals*. New York: American Geographical Society.

Scarcelli N, Tostain S, Mariac C, *et al.* 2006. Genetic nature of yams (*Dioscorea* sp.) domesticated by farmers in Benin (West Africa). *Genetic Resources and Crop Evolution* 53: 121–130.

Scarcelli N, Cubry P, Akakpo R, *et al.* 2019. Yam genomics supports West Africa as a major cradle of crop domestication. *Science Advances* 5: eaaw1947.

Schrieber M, Stein N, Mascher M. 2018. Genomic approaches for studying crop evolution. *Genome Biology* 19: 140-154.

Silvertown J. 2008. The evolutionary maintenance of sexual reproduction: evidence from the ecological distribution of asexual reproduction in clonal plants. *International Journal of Plant Science* 169: 157-168.

Sonnante G, Hammer K, Pignone D. 2009. From the cradle of agriculture a handful of lentils: history of domestication. *Rendiconti Lincei* 20: 21-37

Smith BD, Yarnell RA. 2009. Initial formation of an indigenous crop complex in eastern North America at 3800 BP. *Proceedings of the National Academy of Sciences* 106: 6561-6566.

Smýkal P, Nelson M, Berger JD, Wettberg E. 2018. The impact of genetic changes during crop domestication on healthy food development. *Agronomy* 8: 26.

Smýkal P, Coyne CJ, Ambrose MJ, *et al.* 2015. Legume crops phylogeny and genetic diversity for science and breeding. *Critical Reviews in Plant Sciences* 34: 43-104.

Stebbins GL. 1950. *Variation and Evolution in Plants.* New York: Colombia University Press.

Stitzer MC. and Ross-Ibarra J. 2018. Maize domestication and gene interaction. *New Phytologist* 220: 395-408.

Streck NA, Pinheiro DG, Zanon AJ, *et al.* 2017. Effect of plant spacing on growth, development and yield of cassava in a subtropical environment. *Crop Production and Management* 75: 407-415.

Sunell LA, Healey PL. 1979. Distribution of calcium oxalate crystal idioblasts in corms of taro (*Colocasia esculenta*). *American Journal of Botany* 66: 1029–32.

Sunell LA, Healey PL. 1985. Distribution of calcium oxalate crystal idioblasts in leaves of taro (*Colocasia esculenta*). *American Journal of Botany* 72: 1854–1860.

Tanno K, Willcox G. 2012. Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Vegetation History and Archaeobotany* 21: 107-115.

Terrell JE, Hart JP, Barut S, *et al.* 2003. Domesticated landscapes: the subsistence ecology of plant and animal domestication. *Journal of Archaeological Method and Theory* 10: 323-368.

Trněný O, Brus J, Hradilová I, *et al.* 2018. Molecular evidence for two domestication events in the pea crop. *Genes* 9: 535. doi:10.3390/genes9110535.

Torrence R, Barton H, eds., 2006. *Ancient Starch Research*. Walnut Creek, CA: Left Coast Press.

Ugent D, Peterson LW. 1988. Archaeological remains of potato and sweet potato in Peru. *Circular (International Potato Center)* 16: 1-10.

Ugent D, Pozorski S, Pozorski T. 1981. Prehistoric remains of the sweet potato from the Casma Valley of Peru. *Phytologia* 49: 401-415.

Ugent D, Pozorski S, Pozorski T. 1982. Archaeological potato tuber remains from the Casma Valley of Peru. *Economic Botany* 36: 182-192.

Ugent D, Pozorski S, Pozorski T. 1984. New evidence for ancient cultivation of *Canna edulis* in Peru. *Economic Botany* 38: 417-432.

Ugent D, Pozorski S, Pozorski T. 1986. Archaeological manioc (*Manihot*) from coastal Peru. *Economic Botany* 40: 78-102.

Van der Veen M, Morales J. 2011. Summer crops – from trade to innovation. In: Van der Veen M. ed., *Consumption, Trade and Innovation. Exploring the Botanical Remains from the Roman and Islamic Ports at Quseir al-Qadim, Egypt*. Frankfurt: Africa Magna Verlag, pp. 75-119.

van Oss R, Abbo S, Eshed R, Sherman A, Coyne CJ, Vandemark GJ, et al. 2015. Genetic relationships in *Cicer* sp. expose evidence for geneflow between the cultigen and its wild progenitor. *PLoS ONE* 10(10): e0139789

Vaughan DA, Balazs E, Heslop-Harrison JS. 2007. From crop domestication to super-domestication. *Annals of Botany* 100: 893-901.

Vernier P, Orkwor GC, Dossou AR. 2003. Studies of yam domestication and farmers' practices in Benin and Nigeria. *Outlook on Agriculture* 32: 35-41.

Vrydaghs L, Swennen RR, Mbida C, Doutrelepont H, De Langhe E, de Maret, P. 2003. The banana phytolith as a direct marker of early agriculture: A review of the evidence. In: Hart DM, Willis LA eds., *Phytolith and Starch Research in the Australia - Pacific - Asian Regions: The State of the Art*. *Terra Australis* 19. Canberra: Pandanus Books, pp. 175-185.

Vrydaghs L, Ball TB, Volkaert H, Van Den Houwe I, Manwaring J, De Langhe E. 2009. Differentiating the volcaniform phytoliths of bananas: *Musa acuminata. Ethnobotany Research & Applications* 7: 239-246.

Wang W, Feng B, Xiao J, *et al.* 2014. Cassava genome from a wild ancestor of cultivate varieties. *Nature Communications* 5: 5110.

Williams GC. 1975. *Sex and Evolution*. Princeton: Princeton University Press.

Winchell F, Stevens CJ, Murphy C, Champion L, Fuller DQ. 2017. Evidence for sorghum domestication in Fourth Millennium BC eastern Sudan: Spikelet morphology from ceramic impressions of the Butana Group. *Current Anthropology* 58: 673-683.

Yen DE. 1973. The origins of Oceanic agriculture. *Archaeology and Physical Anthropology in Oceania* 8: 68-85.

Yen DE. 1974. *The Sweet Potato and Oceania: An Essay in Ethnobotany*. Honolulu: Bishop Museum Bulletin 236.

Yen DE. 1989. The domestication of environment. In: Harris DR, Hillman GC, eds., *Foraging and Farming: The Evolution of Plant Exploitation*. London: Unwin Hyman, pp. 55-75.

Zannou A, Richards P, Struik PC. 2006. Knowledge of yam variety development: insights from farmers' and researchers' practices. *Knowledge Management for Development Journal* 2: 30-39.

Zohary D. 1984. Modes of evolution in plants under domestication. In: Grant WF, ed., *Plant Biosystematics.* New York: Academic Press, pp. 579-586.

Zohary D. and Hopf M. 2000. *Domestication of Plants in the Old World*. Oxford: Oxford University Press.

Zong Y, Yao S, Crawford GW, *et al.* 2017. Selection for oil content during soybean domestication revealed by X-ray tomography of ancient beans. *Scientific Reports 7*: 43595.

Captions

Figure 1. Loci of domestication for globally significant food crops (upper; after Fuller et al. 2014: Fig.1) and annual global production (lower; FAO 2016) for major agricultural crops grown in fields (monoculture) and plots (polyculture). Excludes arboricultural/silvicultural crops, such as trees, palms and pandanus, and fodder crops. Groups of crops are colour-coded according to: sexually-reproduced cereals (blue); sexually-reproduced legumes and vegetables (green); and, vegetatively-propagated bananas, root crops and sugarcane (orange). Notes: 1. In map (upper) * connotes plants likely moved as a weed from region of origin and domesticated in another locale; oats (*Avena sativa*) and rye (*Secale cereale*) originated in Southwest Asia and were probably domesticated in eastern-central Europe during the late Holocene. 2. In graph (lower), yield of sugarcane may represent total crop biomass, while other crops are usually given as primary product only.

Figure 2. Comparison of the unilinear domestication episode for barley (upper; *Hordeum vulgare*) with the multi-staged and stepwise domestication trajectory for bananas (lower; *Musa* cvs.). Upper: the domestication episode for barley (*Hordeum vulgare*) extends from c.11,500 cal BP to c. 8500 cal BP and is reconstructed from archaeobotanical evidence at multiple sites for percentages of non-shattering cultivars (red) and increasing grain breadth (blue; Fuller et al. 2014: Tables S2-S3). Lower: rates of change in domesticatory traits are inferred to increase across three thresholds: early planting of diploid cultiwilds; hybridisation to generate diploid cultivars; and, triploidisation with subsequent widespread dispersal (Perrier et al. 2011; De Langhe et al. 2015).

Figure 3. Microfossil techniques for the investigation of vegetatively propagated crops. A. Photomicrograph of starch granule of *Disocorea hispida* indicating diagnostic elements: h=hilum and l=lamellae (modern reference sample). B. Photomicrograph of volcaniform phytolith of AAw banana (*Musa* sp.; modern reference sample from Ngezi Forest, Pemba). C. Photomicrograph of transverse section through a sugarcane (*Saccharum officinarum*) stem fragment from a 200-300 year-old domestic context at Kuk Swamp (Lewis et al. 2016: Fig. 3d).

Figure 4. Archaeobotanical techniques for the investigation of calcium oxalate in taro (*C. esculenta*). A. MicroCT visualisation of parenchyma fragment with low density areas in blue (cell walls) and high density areas in red (druses and raphide bundles comprising calcium oxalate crystals). B. MicroCT visualisation showing distribution of high density areas in A. C-D. SEM images of taro parenchyma with druses visible as lighter concentrations. E. Photomicrograph of cell packed with raphides. F. Photomicrograph of raphide showing needle-like morphology and asymmetric proximal tip (lower right). All images are from modern reference samples.

Table 1. Expected differences between asexually and sexually produced offspring (after Williams 1975)†

Asexual offspring	Sexual offspring
Mitotically standardised	Meiotically diversified
Produced more continuously	Seasonally limited
Develop close to parent	More widely dispersed
Develop more immediately	Often more dormant
Develop more directly to reproductive stage	Develop more slowly through a non-reproductive stage
Phenotype and optimum genotype predictable from those of parent	Phenotype and genotype less predictable
Low mortality rate	High mortality rate

†From Abrahamson (1980: Table 5.2)

Table 2. Domestication traits in sexually vs asexually-reproduced plants. Sexually-reproduced plants include cereals, legumes, leafy vegetables, and many fruit and nut trees; asexually-reproduced plants include root crops, grasses and vegetables, as well as palms, pandanus and trees. While propagation may be predominantly sexual or asexual for a given crop, many crop taxa reproduce naturally using both modes of reproduction. When one form or the other of propagation is favoured for a crop that has both modes of reproduction, the dominance of one form of reproduction is the focus of selection and constitutes a domestication trait.

Trait category	Domestication in sexually propagated plants	Domestication in asexually propagated plants
Mode of reproduction	1. Partial or complete loss of asexual reproduction ability 2. Increased uniformity in seed germination traits; loss of dormancy	1. Partial or complete loss of sexual reproduction ability 2. Increased uniformity in clonal reproduction traits
Plant life-cycle	Shift towards annual lifecycle based on sexual reproduction from seed	Shift towards perennial lifecycle based on vegetative production of suckers, shoots, vegetative storage organs (USOs) and other viable plant parts
Yield of edible portion	1. Increased size in seeds of cereals, legumes, nuts, stone fruits 2. Increased number of fruits and seeds 3. Increased ratio of edible to non-edible plant parts in whole plant	1. Increased size of edible vegetative storage organs (often the organ used for clonal propagation) 2. Increased number of edible organs 3. Increased ratio of edible to non-edible plant parts in whole plant.
Ease of harvesting	Development of non-shattering seed heads/pods	Development of bunched or fused vegetative storage organs Development of easily separated USOs/bud separation
Timing of production	Synchronous production of harvested parts within plant and between plants	Asynchronous and more continuous production of harvested parts, with in-ground storage for some USOs
Plant architecture	Changes in: Apical dominance Branch arrangements Leaf arrangements	Changes in: Apical dominance Branch arrangements Leaf arrangements

Defensive adaptations	Loss of defensive adaptations (spines, hard seed casings, toxicity, acridity) to enhance harvesting, processing and consumption	Loss of defensive adaptations (spines, hard seed casings, toxicity, acridity) to enhance harvesting, processing and consumption
Pre-Domestication Traits		
Ease of storage	1. Traits that favour survival of seeds used for propagation 2. Traits that favour preservation of seeds used for consumption	1. Traits that favour survival of USOs used for propagation 2. Traits that favour preservation of USOs used for consumption
Post-Domestication Trait	**Improvement/diversification/dispersal**	
Photoperiod sensitivity	Changes in photoperiod sensitivity according to latitude, reproductive cycle of the wildtype, and latitudinal origin of wildtype	Changes in photoperiod sensitivity according to latitude and reproductive cycle of the wildtype, and latitudinal origin of wildtype
Environmental tolerance	Traits that enable cultivation in wider environmental range (altitudinal, latitudinal, water conditions, wind conditions, and soil type)	Traits that enable cultivation in wider environmental range (altitudinal, latitudinal, water conditions, wind conditions, and soil type)
Disease resistance	Reduced resistance to disease and pests due to human selection following continued sexual reproduction of sub-population	Dramatic reduction in resistance to disease and pests due to low genetic variability in clonally reproduced cultivars (despite somatic mutation)
Palatability	Selection for various desired traits, often involving a loss of defensive chemical adaptations	Selection for various desired traits, often involving a loss of defensive chemical adaptations
Processing	Selection for reduction or ease of removal of inedible portions (free-threshing cereals, seed integument, nutshells, pod shells)	Selection for reduction or ease of removal of inedible portions (skin, fibre)

Table 3. Parenchymatous storage organs in non-woody plants exploited by people and ordinarily propagated vegetatively, primarily underground storage organs (USOs) (after Abrahamson 1980; Hather 1998, 1994a, 2000). Classifications are not necessarily exclusive for a particular plant, given changes in plant structures during lifecycles, such as rhizome-caudex in *Typha* spp.: Hather 2000: 16). Many USOs are exploited by people for food and used for propagation; however, this is not always the case. For example, bananas (*Musa* cvs.) are exploited for fruit and reproduced from suckers growing from a corm at the base of the pseudo-stem, while sweet potato (*Ipomoea batatas*) is exploited for root tubers and can be reproduced from root tubers and vine slips (stem cuttings).

Plant structure	Description	Examples
Bulb	Rounded underground storage organ comprised of a short stem surrounded by fleshy scale leaves or leaf bases	Garlic (*Allium sativum*); Lilly (*Lilium* spp.); Onion (*Allium cepa*)
Bulbil	Tuber produced in the axil of a leaf capable of adventitious root growth. Propagation by fragmentation and adventitious growth	Bitter/cheeky yam (*Dioscorea bulbifera*)
Caudex	Vertical multimodal swelling of a stem base. Sometimes referred to as pachycaul stem. This may or may not constitute the reproductive structure of the plant.	Baobab (*Adansonia* spp.); Cycads (*Cycas* spp., *Zamia* spp.); Giant taro (*Alocasia macrorrhiza*); Tree ferns (*Alsophila* spp.)
Corm	Vertical multimodal tuber of one year or more duration, producing ephemeral shoots. Each node on a corm has the capacity to produce daughter corms. Propagation by axillary replacement, fragmentation and adventitious growth.	Canna (*Canna edulis*); Cocoyam (*Xanthosoma saggitifolium*); Eddoe (*Colocasia antiquorum*); Elephant foot yam (*Amorphophallus* spp.); Enset(*Ensete ventricosum*); Fern (e.g. *Pteridium esculentum*); Swamp taro (*Cyrtosperma merkusii*); Taro (*Colocasia esculenta*); Water chestnut (*Eleocharis dulcis*)

Rhizome	Perennial horizontal axis more or less homogenously swollen or unswollen supporting ephemeral leaves and flowering axes arising vertically at nodes. Propagation by fragmentation and adventitious growth.	Arrowroot (*Maranta arundinacea*); Galangal (*Alpina* sp.); Ginger (*Zingiber officinale*); Oca (*Oxalis tuberosa*); Tumeric (*Curcuma* sp.); Typha (*Typha* spp.)
Rhizome tuber	Multiple swollen regions along the length of, or terminally attached to, a rhizomatous axis. Propagation by fragmentation and adventitious growth.	Cyperus (*Cyperus* spp.), *Scirpus* spp.
Root tuber	Swollen regions along the length of an otherwise unswollen root system. Occasional vegetative propagative capability by adventitious growth	Cassava/Manioc (*Manihot esculenta*); Leren (*Calathea allouia*); *Murnong* (*Microseris scapigera*); Pencil yam (*Vigna lanceolata*); Sweet potato (*Ipomoea batatas*)
Stolon tuber	Swollen regions along the length of, and terminally attached to, a stolon. In the yams, swelling may be massive forming large, long or thick tubers. Propagation by fragmentation and adventitious growth.	Arrow head (*Sagittaria sagittifolia*); *Plectranthus* spp.; Lotus root (*Nelumbo nucifera*); Potato (*Solanum tuberosum*); Yams (*Dioscorea* spp.)

Note:

1. Tap roots are excluded here, as although a swollen secondary root of a biennial or perennial herbaceous plant, the crops are ordinarily reproduced from seed, as a tap root has no vegetative propagative capability.

Triticum spp.
Pisum sativum
Avena sativa*
Hordeum vulgare
Secale cereale*
Cicer arietinum

Glycine max
Panicum miliaceum
Setaria italica

Oryza sativa
ssp. indica

Oryza sativa
ssp. japonica

Zea mays

Capsicum spp.

Pennisetum
glaucum

Ipomoea
batatas

Vigna
radiata

Cucurbita spp.
Dioscorea spp.
Phaseolus spp.

Dioscorea spp.

Sorghum
bicolor

Solanum
tuberosum

Manihot
esculenta

Saccharum officinarum
Musa cvs.
Dioscorea spp.
Colocasia esculenta

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Early Holocene
Mid Holocene
Domesticatory
disposition

Cereal
Vegetable, legume
Root crop, cane grass, banana

million tonnes

	0	200	400	600	800	1,000	1,600	1,800	2,000

sugarcane — Saccharum officinarum
maize — Zea mays
wheat — Triticum spp.
rice (paddy) — Oryza sativa
potato — Solanum tuberosum
soybean — Glycine max
manioc — Manihot esculenta
melons — Cucurbitaceae
bananas — Musa cvs.
sweet potato — Ipomoea batatas
yams — Dioscorea spp.
sorghum — Sorghum bicolor
beans — Fabaceae (Phaseolus spp., Vigna radiata)
plantain — Musa cvs.
chillies/peppers — Capsicum spp.
pea — Pisum sativum
millets — Panicum miliaceum, Setaria italica, Pennisetum glaucum
cucurbits — Cucurbitaceae
oats — Avena sativa
barley — Hordeum vulgare
rye — Secale cereale
chickpea — Cicer arietinum
taro — Colocasia esculenta