

The domestication syndrome in vegetatively propagated field crops

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- **Background** Vegetatively propagated crops are globally significant in terms of current agricultural production, as well as for 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 with sexually reproduced crops, especially cereals and legumes, the domestication syndrome in vegetatively propagated field crops is poorly defined.
- **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 for domestication for vegetatively propagated field crops in the past.
- **Conclusions** Although convergent phenotypic traits are identified, none of them 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’.

Key words: Asexual (clonal) reproduction, vegetative propagation, phenotype, early agriculture, developmental plasticity, archaeobotany.

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 sub-tropics. 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.) (Fig. 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, 1998; 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).

The domestication histories and status of several vegetatively propagated plants are confounded because no known wild ancestor exists, for example greater yam (*Dioscorea 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

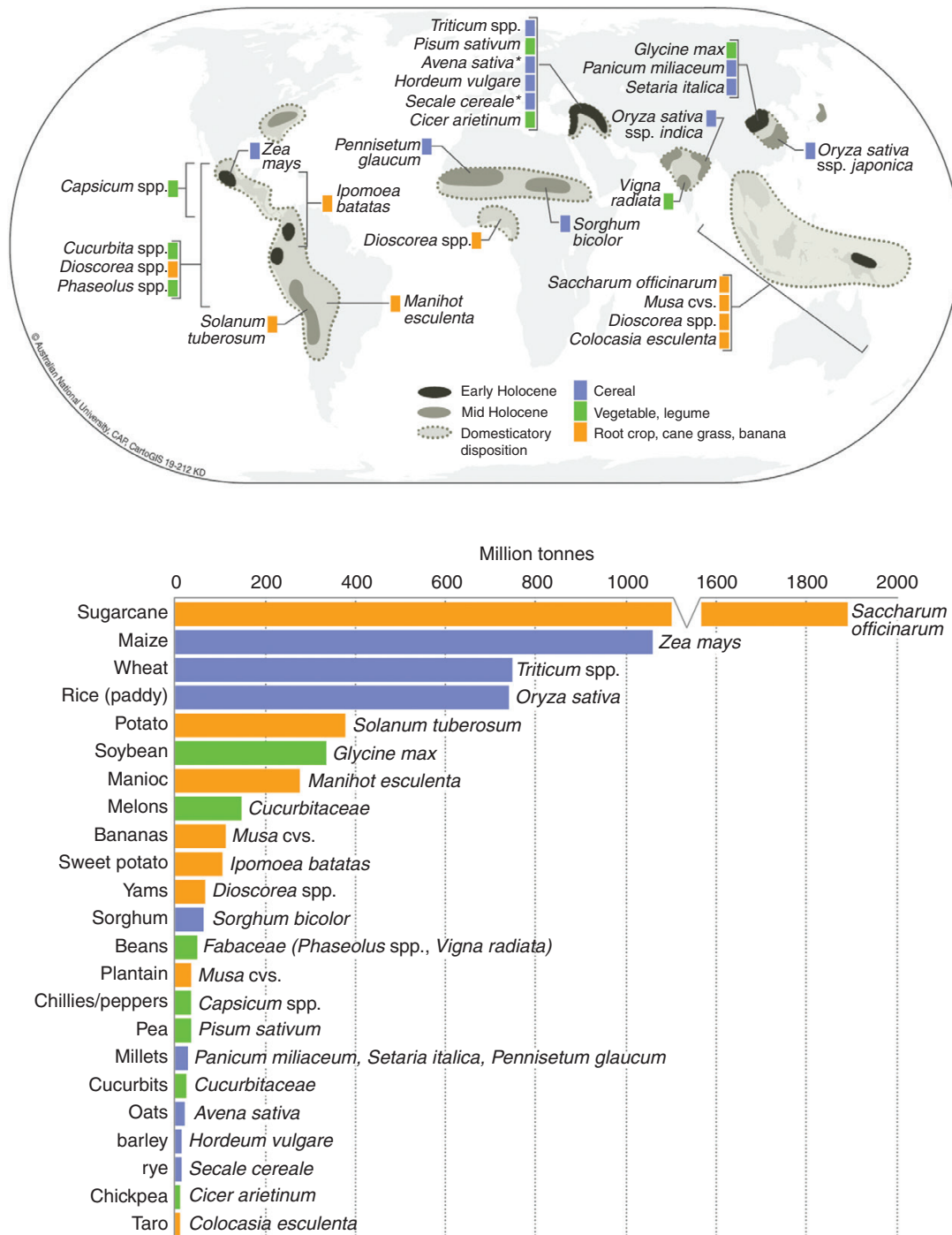


FIG. 1. Loci of domestication for globally significant food crops (upper; after Fuller *et al.*, 2014; fig. 1) and annual global production (lower; FAO, 2016) for major agricultural crops grown in fields (monoculture) and plots (polyculture). Arboricultural/silvicultural crops, such as trees, palms and pandanus, and fodder crops are excluded. 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 the map (upper), an asterisk connotes that plants probably moved as a weed from region of origin and domesticated in another locale; oats (*Avena sativa*) and rye (*Secale cereale*) originated in South-west Asia and were probably domesticated in eastern-central Europe during the late Holocene. 2. In the graph (lower), yield of sugarcane may represent total crop biomass, while other crops are usually given as primary product only.

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 interspecific or intrasub-specific hybridization reflecting sexual reproduction, such as AA diploid banana cultivars (*Musa*), sugarcane (members of the *Saccharum* complex) and potatoes (members of the *Solanum brevicaulis* complex). Diploid hybridization 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 characterize 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 cultivation and 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 (Fig. 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 fertilized 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 South-east Asia; wheat (*Triticum* spp.) and barley (*Hordeum vulgare*) in South-west 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 South-west Asia; beans (*Phaseolus* spp.) in the Americas (Rendón-Anaya et al., 2017); soybean (*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; Abbo et al., 2014; 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; Murgia et al., 2017), with other changes considered to be more loosely related to plant evolution under cultivation. However, such an approach pre-supposes 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 sub-set of sexually reproducing crops, primarily cereals (Allaby et al., 2018; Kistler et al., 2018; Schreiber et al., 2018; Stitzer and Ross-Ibarra, 2018; Scott et al., 2019) and legumes (Smýkal et al., 2015; Bitocchi et al., 2017). However, most ancient DNA has been obtained from derived cultivars rather than from the oldest domesticated plant remains. Clear physical changes in morphological architectures associated with reproduction and propagation, namely non-shattering rachis of barley (Fig. 2), wheat (Tanno and Wilcox, 2012), rice (Fuller et al., 2009; Barron et al., 2017) and sorghum (Winchell et al., 2017), as well as the rapid evolution of the cob in maize (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 (Araceae), 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, early domestication and global agriculture.

Vegetative propagation is especially important for unravelling the history of early cultivation and domesticatory practices in the wet tropics and sub-tropics, mountainous regions, wetland habitats and deserts (Harris, 1972). For instance, several regionally important crop plant assemblages are based

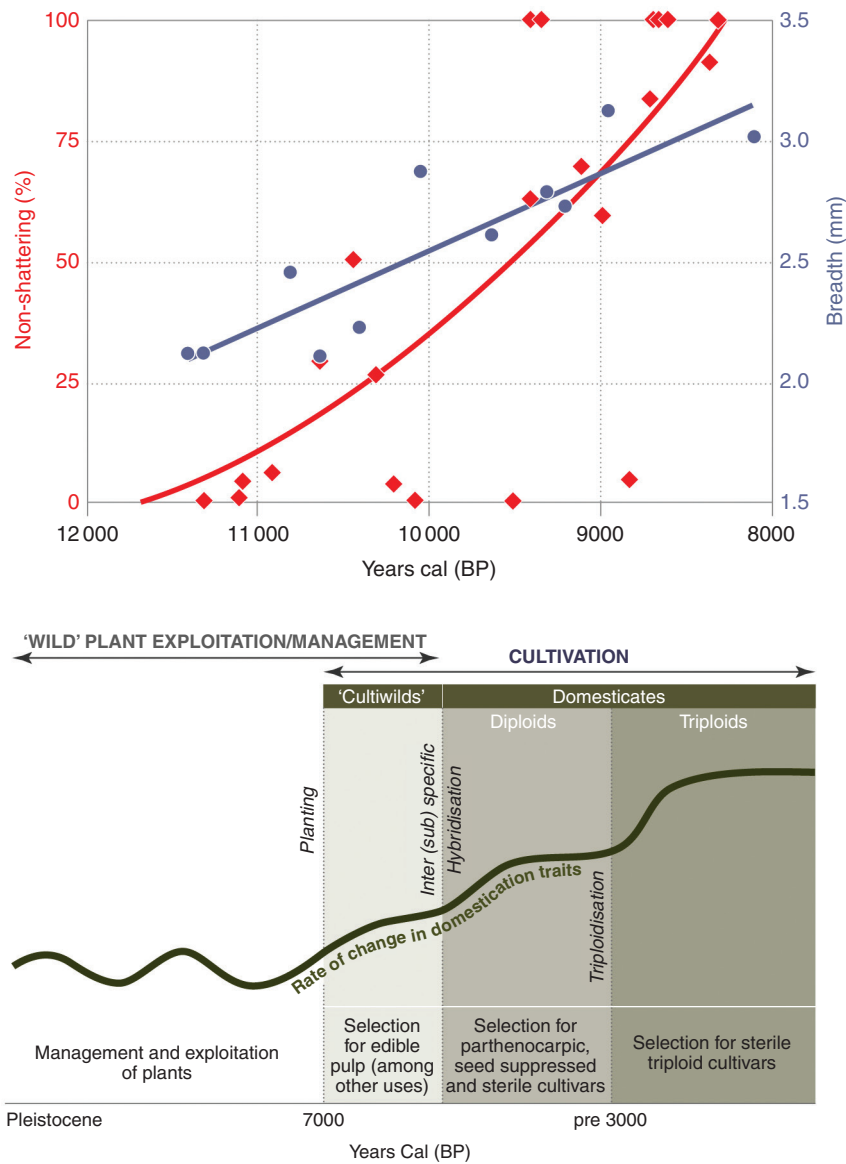


FIG. 2. Comparison of the unilinear domestication episode for barley (upper; *Hordeum vulgare*) with the multistaged and stepwise domestication trajectory for bananas (lower; *Musa cvs*). Upper: the domestication episode for barley (*Hordeum vulgare*) potentially extends from approx. 11 500 cal BP to approx. 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 and S3). Lower: rates of change in domesticatory traits are inferred to increase across three thresholds: early planting of diploid cultiwilds; hybridization to generate diploid cultivars; and triploidization with subsequent widespread dispersal (Perrier et al., 2011; De Langhe et al., 2015).

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*), *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* and *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 (*C. 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 characterized 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 15th 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 (Mbida et al., 2001) and Iberia (Dozy, 1961) to eastern Polynesia (Yen, 1973); and taro (*C. esculenta*) spread from uncertain homelands in South-east 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 pre-historic 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 characterization 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 (Chair *et al.*, 2016) and some yams (Scarcelli *et al.*, 2019); an exception is the banana which is present in many archaeological phytolith records (Fig. 2; Perrier *et al.*, 2011; Castillo and Fuller, 2016).

ASEXUAL REPRODUCTION IN PLANTS

Many plants have two modes of reproduction: sexual reproduction from fertilized seed; and asexual reproduction, i.e. clonal growth through regeneration from plant structures (Stebbins, 1950; Harper, 1977; Abrahamson, 1980). Asexual reproduction by-passes pollination and production of fertilized seed; instead, offspring genetically identical to the parent plant, namely clones, are produced by processes that are more akin to growth than to reproduction (Abrahamson, 1980: p. 89). In trying to characterize 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: p. 157). Apomictic seeds are clones of the mother plant that are packaged and dispersed in the trappings of sexually produced progeny (Silverton, 2008: pp. 457–458). They differ from ramets in that they still go through the same developmental programme (seedling, juvenile and reproductive adult stages) as any other seed propagation cycle. Manioc is capable of apomixis (Ellstrand, 2003: p. 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 with seedlings because propagules are better provisioned initially with a larger food supply (Table 1; Abrahamson, 1980: p. 96) and may even start as miniature versions of the parent plant with developed root systems (Silverton, 2008: p. 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 (Abrahamson, 1980: p. 96). Through vegetative reproduction, individual genetic lineages may be extremely long lived; the aspen (*Populus tremuloides*) colony in southern Utah, known colloquially as ‘Pando’, is approx. 8000–10 000 years old (Mock *et al.*, 2008: p. 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

TABLE 1. *Expected differences between asexually and sexually produced offspring (adapted from Williams, 1975 and Abrahamson, 1980: table 5.2)*

Asexual offspring	Sexual offspring
Mitotically standardized	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

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 recolonize newly burned habitat (Abrahamson, 1980: p. 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 (Hather, 1996).

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 either through genetic changes, involving some degree of sexual recombination or mutation, or through more immediate genetic expression within changed ecological conditions that influence the ‘plasticity’ of growth form (de Kroon *et al.*, 1994: pp. 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 colonize new habitats outside of the natural range in which flowering occurs and where pollinators are absent (Abrahamson, 1980: p. 963). It also has the potential to remove plants away 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 their natural range), new phenotypes of individual species and through the spontaneous creation of new hybrids of related species, i.e. sympatric hybridization (Clement *et al.*, 2010).

Arguably, vegetative propagation can be characterized as a form of instant domestication (Stetter *et al.*, 2017) that enables more controlled selection of favoured phenotypic characteristics than under sexual reproduction. In theory, vegetative propagation enables instantaneous genetic isolation of preferred phenotypes; in practice, though, spontaneous sexually reproduced progeny may also be incorporated into clonally reproduced crop assemblages thereby enabling gene flow and potentially prolonging the period of domestication. 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 interannual reliability of production); ease of processing (such as a hard seed coat or nut casing, extraction of the edible portion or spininess); ease of cooking (pounding, soaking, heating, roasting, etc.); and selection for secondary characteristics such as toxicity, acidity, 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 incomplete, these phenotypic commonalities can be tentatively compared with 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 that 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 to become dominant in cultivars in numerous ways. Natural processes such as spontaneous mutations, polyploidization and hybridization

combined with preferential anthropic selection of parthenocarpic, seed-suppressed and seedless forms have led to hybrid dysfunction, reproductive dysfunction and potential loss of capacity for sexual reproduction. 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 preferentially utilized 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 (*D. alata*; Alexander and Coursey, 1969) and Ethiopian domesticated enset (*E. ventricosum*; Hildebrand, 2003; Borrell *et al.*, 2019). In 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 fertilization (Gustafson, 1942). 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 reproduce sexually, 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 fertilized, as occurs in many fig varieties (*Ficus carica*; Condit, 1947). Anthropic selection of parthenocarpic forms of diploid banana (*Musa* cvs) in the South-east 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, or the seed reduction in enset cultivars (Hildebrand, 2003).

Hybrid dysfunction leading to sterility is a possible factor underlying vegetative domestication. Introgression, or hybridization, 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 polyploidization 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 probably developed spontaneously, such as when cultivated banana diploids were brought together or into contact with other cultivated or wild diploids (Perrier *et al.*, 2011).

Polyploidy, though, should not be considered a domestication trait. 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

TABLE 2. Domestication traits in sexually vs. asexually reproduced plants

Trait category	Domestication in sexually propagated plants	Domestication in asexually propagated plants
Mode of reproduction	1. Partial or complete loss of asexual reproduction ability	1. Partial or complete loss of sexual reproduction ability
Plant life cycle	2. Increased uniformity in seed germination traits; loss of dormancy Shift towards annual life cycle based on sexual reproduction from seed	2. Increased uniformity in clonal reproduction traits Shift towards perennial life cycle based on vegetative production of suckers, shoots, underground storage organs (USOs) and other viable plant parts
Yield of edible portion	1. Increased size in seeds of cereals, legumes, nuts and stone fruits 2. Increased number of fruits and seeds 3. Increased ratio of edible to non-edible plant parts in a 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 a whole plant
Ease of harvesting	Development of non-shattering seed heads/pods	Development of bunched or fused vegetative storage organs
Timing of production	Synchronous production of harvested parts within a plant and between plants	Development of easily separated USOs/bud separation 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, acidity) to enhance harvesting, processing and consumption	Loss of defensive adaptations (spines, hard seed casings, toxicity, acidity) 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 traits		
Improvement/diversification/dispersal		
Photoperiod sensitivity	Changes in photoperiod sensitivity according to latitude, reproductive cycle of the wild type and latitudinal origin of the wild type	Changes in photoperiod sensitivity according to latitude and reproductive cycle of the wild type and latitudinal origin of the wild type
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 and pod shells)	Selection for reduction or ease of removal of inedible portions (skin and fibre)

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. Note that in many clonally propagated fruit trees, fertilization is still essential for crop production. 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.

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 tolerance 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*) and taro (*C. esculenta*) cultivars (Kennedy and Clarke, 2004). As McKey *et al.* (2010) observed, cultivated stock of many vegetative crops reflects clonal and sometimes spontaneous sexual reproduction; the different reproductive strategies

have 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, triploidy/polyploidy and 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 in vegetatively propagated field crops. 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, such as 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 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 to be 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 and 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. Seed suppression has also been noted in some sexually reproduced crops, such as some varieties of cultivated citrus fruits (*Citrus* spp.; Roose et al., 1995) and chempedak (*Artocarpus integer*; Primack, 1985). In other edible fruits, increased seed size occurred with domestication (Fuller, 2018), even if later suppression of seeds became possible with vegetative reproduction, for example in date palms (*Phoenix*

dactylifera) and grapes (*Vitis vinifera*). In a few 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). These morphological changes can be attributed in part to plastic responses on the part of plants to reduced soil nutrient levels, when increased root surface to volume ratios, i.e. longer thinner roots, allow a plant to take up more minerals from its rhizosphere; this has been characterized as ‘plant nutrient-foraging plasticity’ (Sultan, 2015: p. 81; see also Hodge, 2014). Phenotypic variability, which may be linked to subtle environmental differences, as well as likely gene flow between wild and cultivated yams, often makes definition of domesticated, feral and wild populations extremely difficult (Scarcelli et al., 2006; cf. Scarcelli et al., 2019).

Ease of harvesting

The development 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), berries (*Rubus* spp.), breadfruit (*A. altilis*), figs (*F. carica*) and pandanus (*Pandanus* spp.). In contrast, there is a tendency for greater separation amongst USOs – such as in potatoes (*S. tuberosum*), sweet potatoes (*I. batatas*) and yams (*Dioscorea* spp.) – especially in more friable, cultivated soils, which is plausibly a plastic response to growth environment as much as the product of genetic change. The contrasting fusion of fruit/nuts vs. separation in USOs probably 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 sub-tropical 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:

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)*

Plant structure	Description	Examples
Bulb	Rounded underground storage organ comprised of a short stem surrounded by fleshy scale leaves or leaf bases	Garlic (<i>Allium sativum</i>); lily (<i>Lilium</i> spp.); onion (<i>Allium cepa</i>)
Bulbil	Tuber produced in the axil of a leaf capable of adventitious root growth. Propagation by fragmentation and adventitious growth	Bitter/cheeky yam (<i>Dioscorea bulbifera</i>)
Caudex	Vertical multimodal swelling of a stem base. Sometimes referred to as a pachycaul stem. This may or may not constitute the reproductive structure of the plant	Baobab (<i>Adansonia</i> spp.); cycads (<i>Cycas</i> spp., <i>Zamia</i> spp.); giant taro (<i>Alocasia macrorrhiza</i>); tree ferns (<i>Alsophila</i> spp.)
Corm	Vertical multimodal tuber of 1 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 (<i>Canna edulis</i>); cocoyam (<i>Xanthosoma sagittifolium</i>); eddoe (<i>Colocasia antiquorum</i>); elephant foot yam (<i>Amorphophallus</i> spp.); enset (<i>Ensete ventricosum</i>); fern (e.g. <i>Pteridium esculentum</i>); swamp taro (<i>Cyrtosperma merkusii</i>); taro (<i>Colocasia esculenta</i>); water chestnut (<i>Eleocharis dulcis</i>)
Rhizome	Perennial horizontal axis more or less homogeneously swollen or unswollen supporting ephemeral leaves and flowering axes arising vertically at nodes. Propagation by fragmentation and adventitious growth	Arrowroot (<i>Maranta arundinacea</i>); galangal (<i>Alpinia</i> sp.); ginger (<i>Zingiber officinale</i>); oca (<i>Oxalis tuberosa</i>); tumeric (<i>Curcuma</i> sp.); typha (<i>Typha</i> spp.)
Rhizome tuber	Multiple swollen regions along the length of, or terminally attached to, a rhizomatous axis. Propagation by fragmentation and adventitious growth	Cyperus (<i>Cyperus</i> spp.); <i>Scirpus</i> spp.
Root tuber	Swollen regions along the length of an otherwise unswollen root system. Occasional vegetative propagative capability by adventitious growth	Cassava/manioc (<i>Manihot esculenta</i>); leren (<i>Calathea allouia</i>); murnong (<i>Microseris scapigera</i>); pencil yam (<i>Vigna lanceolata</i>); sweet potato (<i>Ipomoea batatas</i>)
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 (<i>Sagittaria sagittifolia</i>); <i>Plectranthus</i> spp.; lotus root (<i>Nelumbo nucifera</i>); potato (<i>Solanum tuberosum</i>); yams (<i>Dioscorea</i> spp.)

Classifications are not necessarily exclusive for a particular plant, given changes in plant structures during life cycles, such as rhizome–caudex in *Typha* spp.: Hather, 2000: p. 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 pseudostem, while sweet potato (*Ipomoea batatas*) is exploited for root tubers and can be reproduced from root tubers and vine slips (stem cuttings).

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.

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 interplant synchronicity of production and periodicity of fruit production by individual plants (Bourke *et al.*, 2004). Overall, vegetative crop plants display considerable variation: cultivated yams (*Dioscorea* spp.) are persistently photoperiod sensitive despite extensive breeding programmes (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; Fuller *et al.*, 2010). In vegetatively propagated crops, there is much variation: yams have been characterized as exhibiting apical dominance (Coursey, 1967; Passam, 1977), while others propose basal dominance (Mozié, 1984); in manioc (*M. esculenta*), apical dominance becomes more marked with reduced spacing between plants (Streck *et al.*, 2017); and triploid AAB plantains (*Musa cvs*) exhibit more marked apical dominance than diploid and AAA triploid cultivar groups of banana (Ortiz and Vuylsteke, 1994). However, some crops exhibit considerable morphological plasticity, reflecting the growth environment; for instance, wild and cultivated manioc (*M. esculenta*) grow 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 clonal 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*, and *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: p. 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*) also have smoother stalks, as well as fewer raphides (calcium oxalate crystals) and lower to no alkaloid content (Brown, 2000).

Many crops have been selected for reduced acidity, 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.). A secondary metabolite that may impact negatively on human health are cyanogenic glucosides that are hydrolysed by β -glucosidases into hydrocyanic acid (HCN). A single dose of 1–3 mg kg⁻¹ 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 plant species, while others are heterogenous and may contain acyanogenic individuals (Gleadow and Møller, 2014: p. 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: p. 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: p. 171). Pathways to domestication may involve selection of plants with appropriate phenotypic properties, including concentrations of phytochemicals; they may also 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 acid, bitter and toxic varieties is not ubiquitous. In manioc (*M. esculenta*), cultivars are grouped into two main types, sweet and bitter, based on their 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 approx. 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 tapir, 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 pre-domestication and post-domestication processes. For instance, ease of storage is potentially a factor that led foragers 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 (Ladizinsky, 1998; Purugganan and Fuller, 2009; Meyer and Purugganan, 2013). Foremost, the vast phenotypic variation exhibited in most root crops, comprising several hundred cultivars in manioc, potato, taro and sweet potato, among many others, results from centuries and millennia of cultivation. Environmental tolerance, photoperiod sensitivity and disease resistance are also likely to 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 with 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 the 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. The domestication syndrome of convergent traits proposed here for vegetatively propagated crops is, therefore, 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: pp. 125–126). Plasticity is defined as phenotypic change that is environmentally induced, though the direction and the magnitude of that change are 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 an 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) (Figs 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 (e.g. Mercader *et al.*, 2018). Despite these limitations, 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 rain forest (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). Carpological and anthracological remains can further inform on the taxonomic composition of agricultural forests typically integrating vegetatively propagated

bananas, cane grasses and root crops, helping to identify indirect processes of domestication via anthropogenic manipulation of the growth environment.

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: pp. 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). As a result, 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, or 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, waterlogged 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 approx. 4250 to 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 encountered on archaeological sites across the globe, but there have been recurrent problems with obtaining reliable taxonomic identifications (Hather, 1988, 1991, 1994a, b, 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 to 1200 AD (Hather and Kirch, 1991). 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 micro-computed tomography (microCT) and are suggestive of continuities with ethnographic lifestyles in the highlands of New Guinea (Lewis *et al.*, 2016; Pritchard *et al.*, 2018). However, such robust identifications are rare.

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

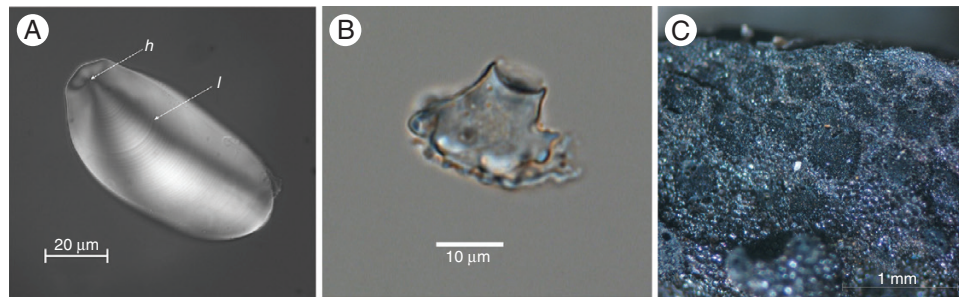


FIG. 3. Microfossil techniques for the investigation of vegetatively propagated crops. (A) Photomicrograph of starch granule of *Disocorea hispida* indicating diagnostic elements: h = hilum, l = lamellae (modern reference sample). (B) Photomicrograph of volcaniform phytolith of an AAw banana (*Musa*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

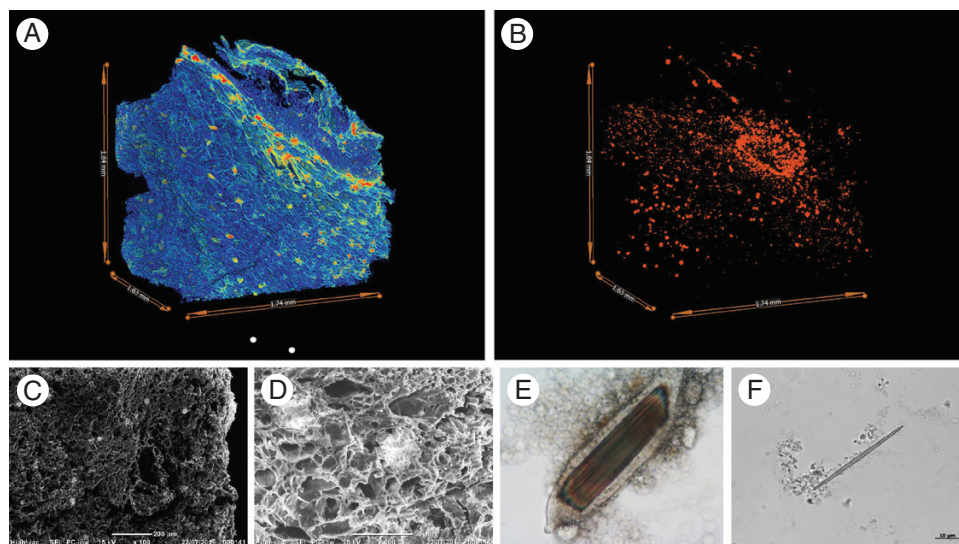


FIG. 4. Archaeobotanical techniques for the investigation of calcium oxalate in taro (*C. esculenta*). (A) MicroCT visualization of a parenchyma fragment with low density areas in blue (cell walls) and high density areas in red (druses and raphide bundles comprising calcium oxalate crystals). (B) MicroCT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

domestication traits in plant macro- and microfossils. 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 thickness and size, as well as starch granule morphology and size, 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 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. In contrast, volcaniform phytoliths in bananas (*Musa* cvs) show an approx. 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 acidity, bitterness, toxicity and other irritants in some tuberous plants are associated with domestication, although contents often vary with life cycle stage (Sunell and Healey, 1979, 1985) and growing conditions, e.g. 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 (Fig. 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 macrofossils 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; Scott *et al.*, 2019).

Equivalent syndrome traits associated with the early domestication of vegetatively propagated crops are not so clear. There are convergent tendencies to lose sexual reproductive capacity and increase the size of the edible portion, although other traits are divergent, and none is ubiquitous. Whereas in sexually reproduced plants phenotypic and genotypic transformations associated with early domestication are portrayed as occurring in lockstep, considerable variation exhibited by vegetatively propagated plants probably represents phenotypic plasticity rather than genotypic variation. Currently, the application of DNA 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 characterized 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. Root growth, in particular, responds

dynamically to soil conditions (Hodge, 2014; Sultan, 2015: pp. 80–81). 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. Hence, although the implications of phenotypic plasticity for charting the early domestication of vegetatively propagated crops are poorly characterized, these do not negate the genetic underpinnings of subsequent crop improvement resulting from millennia of cultivation.

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 human 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, including plant 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 vegetative propagation in the past.

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