



Food items on display at a food fair in Luwingu Zambia

Photo credit: Joe Nkadaani/CIFOR



Fruit Trees in Agroforestry Systems: Complementing Globally Traded Commodities with Local Nutritional Benefits

Meine van Noordwijk, Prasad Hendre, Roeland Kindt, Stepha McMullin, Alice Muchugi, Zacharie Tchoundjeu, Alain Tsobeng, Ramni Jamnadass

Highlights

- Human fruit consumption is below nutritionally recommended levels in most African countries and adding a diverse array of fruit trees as companion trees to globally traded commodity crops such as cocoa or coffee or as main components of agroforestry has potential benefits
- Domestication of locally adapted fruit trees has the potential of providing farmer income, improving nutrition and valorise local diversity, but requires control over tree biology as well as access to land, labour and markets
- Tree biology favours fruits that are unpredictable in occurrence, unattractive until ripe, short-lived afterwards, laxative, but with seeds protected by hard seed coats or toxicity
- Tree domestication tries to achieve a product that is produced regularly and evenly, has a long shelf-life, is nutritionally rich, has no astringent and other unpleasant tastes, and is non-toxic, yet pest-free
- Reconciling the contradicting agendas of trees and people requires skill, persistence and understanding of the underlying biological, social and economic challenges

1. Introduction

All trees are fruit trees, botanically speaking, except for the ‘naked-seed’ Gymnosperms such as conifers-- even though the cones in which edible pine seeds grow are called ‘pine-apples’ (not to be confused with the subsequent use of the same word as a name for *Ananas comosus*). Fruits in Angiosperm (‘enclosed seed’) plants develop from the ovary in which one or more seeds develop and serve to protect the seed from consumers before it is ready to be dispersed,

attract dispersal agents when it is ripe and stimulate that at least some viable seeds reach a location where they have a chance to grow -- surrounded by some readily available nutrient sources. Fruits exist in a wide range of forms across all Angiosperm plant families, with the larger ones logically restricted to trees, shrubs, lianas and other climbers. Trees are not a taxonomic entity but a life form present in more than half the plant families. 'Fruit trees' are thus a rather fuzzy category subject to certain functional and ecological selection forces, rather than having a common origin and shared properties.

In the typical parlour, the term fruit trees is used for trees whose fruits are attractive to humans, providing minerals and vitamins as micro-nutrients and energy sources ('fruit sugars' and/or starch). Fruit production by specific trees tends to be seasonal and -- as explained below -- variable and unpredictable, making it a challenge to provide year-round for the nutritionally recommended daily intake, unless there is sufficient tree diversity within reach. Fruit deficits are especially pronounced in the African continent, despite the high number of species in the local flora plus those introduced from elsewhere. In this chapter, we will provide backgrounds on these issues and on efforts to increase fruit availability through diverse agroforestry systems and domestication of trees that, despite desirable properties of the fruits, don't yet sufficiently match human needs for efficient production.

Attraction, seduction, refusal, commitment, cheating, opportunism against a backdrop of reproduction and survival of the fittest genes -- this is a brief summary of the 'battle of the sexes,' which is good for more than half of the world's literature, poetry, song, dance and film industry. It is, however, also a brief summary of the plant-animal relationship around seed dispersal. From a biological perspective, this is an epic mix of competition and mutualism that, by involving multiple species on both the plant and the animal side, is richer and more varied than the intraspecific battle of sexes. Yet, it gets a small fraction of a percent of human attention, with a few words and concepts spilling over: maturity or ripening. Biologically, it is similar to the pollination relationships that have more sex appeal, but there is an important difference: in seed dispersal, size matters; in pollen, it is stickiness. Although the relation between flowering plants and pollinators and those between fruit producers and their biotic dispersal agents may seem similar, there are several 'game theoretical' differences (Wheelwright and Orians 1982). Plants benefit by directing pollen dispersers to a definite, recognisable target (a conspecific flower), and they can provide incentives at flowers that serve to attract potential pollinators. In contrast, for seeds, the target (an appropriate site for germination and establishment) is seldom readily discernible, and dispersal beneath a conspecific plant may be undesirable. Hence, attachment to animal skin or some time spent inside the animal is functional. A deeper understanding of the biological heritage in the relationship between humans and their preferred fruit trees can help identify some key challenges to a continuous supply of nutritious fruits for human consumption and may point to ways to overcome them.

The priorities of human fruit consumers are different from those of trees as fruit producers, and trying to force trees into human schemes may go against their nature. Answers can be found in being a generalist rather than a specialist when it comes to fruits, enjoying what is there and not worrying about what is not, in a diverse ‘home-garden’ rather than the specialised orchard, for example. In this chapter, we will consider five questions:

- Why do human fruit consumption deficits persist?
- Why do trees produce the fruits?
- Fruit trees on farms: diversity or specialisation?
- What challenges does tree biology pose to domestication?
- What could be the building blocks for targeted research and development?

2. Fruit consumption deficits

The breadfruit (*Artocarpus altilis*) provides starch and was a staple fruit to the people who went island hopping in the Pacific Ocean, leaving traces of the tree as their footprint (Zerega et al 2004). Several tree fruits, such as *Balanites aegyptiaca* (desert dates), *Sclerocarya birrea* (marula) and *Adansonia digitata* (baobab), but also other parts of the same trees (including leaves, young roots) have been famine foods in sub-Saharan Africa (Kenyatta and Henderson 2001, van Noordwijk 1984). However, most of the time, tree fruits are a smaller part of the human diet in terms of calories, but important for minerals and vitamins, as ‘micro-nutrients’. In many parts of sub-Saharan Africa, however, the production and consumption of fruits are inadequate to meet dietary recommendations and to contribute to the alleviation of micronutrient deficiencies and reduction of the risks of several diet-associated diseases (Jamnadas et al 2011, Vira et al 2015). Fruit production needs to increase particularly in regions with low consumption, together with accompanying measures to prevent losses, to provide enough for healthy diets (Harris et al 2021). Seasonal unavailability, inappropriate post-harvest handling and the limited practice of value addition technologies for perishable foods all contribute to the estimated average 58% shortfall in fruit consumption in low-income countries below recommended levels (Siegel et al 2014). The supply-to-need ratio for fruits and vegetables was 1.02, 0.87, 0.63 and 0.42, respectively, for the 43 high-income, 50 upper-middle, 43 lower-middle and 34 low-income countries in the survey (Siegel et al 2014), and 0.78 on average for the 170 countries combined. Consumption of ‘wild foods’ in rural landscapes can be easily underreported (Bharucha and Pretty 2010), especially where young people with high requirements roam around and have customary rights of access to local fruit trees for direct consumption (Coulibaly-Lingani et al 2009, Folefack and Darr 2021). Landscape-level tree cover is positively associated with dietary diversity and fruit and vegetable consumption

(Ickowitz et al 2014), and fruit trees with desirable properties have been actively spread around the tropics. However, their production is seasonal and varies between years, making it hard to secure a reliable supply. Fruits can be less easily ‘outsourced’ than more storable staple foods (van Noordwijk et al 2014). Local production is also desirable, preferably in a well-designed portfolio of different tree species as part of farm and landscape level diversity (McMullin et al 2019). The low predictability of fruit production may, unfortunately, be part of the tree’s hard-wired strategy. Preservation by drying, extraction of juice, fermentation or other means of conservation can prolong the availability of fruits for human consumption. Still, techniques have mostly been developed as part of local knowledge in strongly seasonal climates.

Greater recognition of the role that indigenous fruit tree species could play in delivering key micronutrients in healthier diets requires knowing their nutritional value, especially if they are to be mainstreamed and scaled for their contribution towards better nutrition. However, for some fruit tree species, specifically indigenous species, such data is missing (Stadlmayr et al 2013). This is due to a lack of research, private sector interest and investment in these species, which are often considered underutilised (Dawson et al 2018, van Zonneveld et al 2021). Where data is available for some indigenous species, their nutritional values for certain micronutrients are superior to that of more common, exotic species. For the African species *Adansonia digitata* (baobab), *Sclerocarya birrea* (marula), or *Sorindeia madagascariensis* (grape mango), the vitamin C content can be up to five times higher than for *Citrus sinensis* (orange), which is commonly used (Stadlmayr et al 2019, McMullin et al 2020) as a reference source high in vitamin C. Nutrient content data can be used to inform the selection of a diversity of fruit trees for cultivation, and can be used for dietary assessments, inclusion in food based dietary guidelines (Elmadfa and Meyer 2010) and the selection of nutrient-rich species for domestication programmes.

3. Why do trees produce fruits?

From a plants’ (selfish gene) perspective, fruits are a means (to propagate) and not a goal. The dilemma is that plants are rooted and can’t move -- yet the opportunities for successful establishment of offspring tend to be some distance away from where they grow, and they need at least some non-zero fraction of their seeds to get there. If they target pioneer vegetation or open soil on soils of least moderate soil fertility, their seeds can be small, and wind dispersal is an option. If they target environments where the seed needs a fair amount of energy and nutrient endowment to make it through the early competitive phases with plants already there (or where a big initial investment in roots is needed), seeds have to be large. That in itself implies that

they are attractive targets for predation. They need a packaging that attracts dispersal agents, don't make them stay too long, yet protects the seed while remaining unattractive and full of chemical defence until the time is there for dispersal of viable seeds.

Fruit traits and dispersal agents co-evolved (Gautier-Hion et al 1985), with tropical fruits, with mammal-associated colours (green, orange, brown and yellow) more common in the tropics than at high latitudes and fruit length (a way to increase fruit volume without increasing diameter that determines which animals can swallow the fruit as a whole) increasing towards the tropics (Sinnott-Armstrong et al 2018). Several tropical fruit trees co-evolved with primates and a few other large seed dispersal agents (birds, mammals). A considerable number further co-evolved and co-adapted with the agricultural systems that *Homo sapiens* developed in the past 10,000 years, but very few made it further down the domestication funnel.

Most tree species reach reproductive maturity after a long period of juvenility, and even then, sexual reproduction appears sporadically, often in a mode of masting (Goldschmidt 2013). Seeing plants as 'investment strategists', trees tend to delay reproduction by first focussing on size and the ability to survive adverse seasons, becoming perennial. The investment in flowers, pollination attractants and fruit paraphernalia needs to be balanced with the resources that the seeds get and help them carry through an establishment phase. Fruits are meant to be perishable and have a sharp peak in attractiveness, while many seeds are designed for longevity as appropriate conditions for germination may not match the time frame of fruit ripening and seed dispersal. Variation has been noted in tree flowering and fruiting patterns in natural forests over relatively short distances, with consequences for primate ecology (Harrison et al 2016). Human use of plant resources in agriculture initially focussed on seeds (grains, pulses) and belowground storage organs (roots, tubers and the like) rather than fruits. Extractable oils from fruits and further advanced fermentation products of decomposing fruits (wines) are storable. Some fruits can be dried to slow down decay – these may appear to be ways to cheat on the plants' intent, but as long as humans do take care of seed dispersal and growth of the trees they like, it is a fair deal in evolutionary terms. Maintaining a peak-trough level of fruit availability at the population level is a major plant strategy to avoid the emergence of seed predation specialists. This usually means a strong phenological cycle over the year, with fruit ripening times balancing the best time of year for seeds to germinate, the best periods for active photosynthesis (the sunny, dry season for deep-rooted trees which can afford it) and the lowest risk of predation. Collective action, by synchronising fruit ripening in a short period of time, reduces the risk for all – but may imply a competition for scarce dispersal agents. Active signalling by colour and smell of ripe fruits, while camouflaging unripe fruits among the canopy, is part of the battle for dispersal agents. In the Dipterocarp family, trees only produce fruits once in 5-10 years, for example.

Box 12.1

Geographical origin of important fruit tree species

In contrast to the limited number of primary globally traded tropical commodities, the diversity of fruit trees that can be used as companion trees in agroforestry systems with such commodities is huge. Based on a recent review of major online databases, the single most relevant and globally comprehensive database is the 'World Economic Plants' (WEP) list, intended to be a global list of socioeconomically and culturally valuable species (Khoury et al 2019). Its global lists of socioeconomically and culturally valuable species include 688 plants used as human food under the economic subclass of fruit (GRIN-global 2020). Nearly 60% of this total, 404 fruit species, could be categorised as tree species by matching names with those available in GlobalTreeSearch. To make this comparison, the botanical taxa were standardised with version 2019.05 of the World Flora Online Taxonomic Backbone (WFO 2020, Kindt 2020a) and used to create a species list (please note that GlobalTreeSearch does not include hybrids or plant names of infraspecific levels).

Using the world geographical scheme for recording plant distributions (WGSRPD 2020, Kindt 2020b) to map native countries available from GTS to continents shows that 41% originate in the America's, 39% in Eurasia, 15% in Africa and 4% in the Pacific plus Australasia and 10% with unknown origin. A more detailed list (with species native to more than one of the domains, and total more than 100%):

142 (35.1%) fruit tree species were native to South America, 94 (23.3%) to North America, 133 (32.9%) to Tropical Asia, 105 (26.0%) to temperate Asia, 23 (5.7%) to Europe, 62 (15.3%) to Africa, 18 (4.5%) to the Pacific and 16 (4.0%) to Australasia.

Thus, Africa is not particularly rich in native fruit tree species, but there are still many choices. The global conservation status of 340 of the fruit tree species was classified (Khoury et al 2019) as 140 species of high priority, 196 species of medium priority and only 4 low priority species. There is thus a significant gap in knowledge and domestication activity. For the majority of fruit tree species, information is lacking on their nutrient composition (with only 50 species documented in the USDA Food Composition Database (FDC 2020) and production statistics compiled for only 20 species in the FAOSTAT database (FAO 2020). Twenty-one of these species are listed in the Global Invasive Species Database, but among the non-listed species, there may be risks of invasiveness that need to be considered before taking species outside of their native geography. The species list and details discussed here can be accessed for further analysis (Kindt et al 2021).

The world is yet to tap the full potential of these useful wild species in health and nutrition (van Zonneveld et al 2020). Therefore, the inter- and intra- species diversity conservation is of great importance as future tree improvement programs rely on the available diversity. Currently, only 16 out of the 62 African native fruit tree species are part of the ICRAF Genebank collection.

These inherent properties of strong synchronicity and interannual variability, however, are major challenges for a human society that likes predictability and regular availability to have supply match demand in market value chains. It is typical for fruits to see lots of them wasted

and rotting away, while nearby or shortly before or after, there are fruit consumption deficits from a human health perspective. The farmgate price of fruits tends to be low, except for off-season producers, while end-users pay a pretty high price relative to staple foods. Fruits are luxury foods for urban consumers. Yet, the middlemen and women don't make excessive profit margins: they have to deal with considerable risk of perishability, uncertainty about ripeness-related quality, and expensive storage methods to delay the maturation and decay.

4. Fruit trees on farms

As described in the introduction to the PROSEA volume on edible fruits and nuts of South-East Asia (Table 12.1), five types of cropping/collecting systems can be distinguished, with a large number of species with low average annual productivity involved in opportunistic collecting of wild fruits, and very few tree species (but a considerable 'fanning' at variety level). It is involved in the orchards and corporate plantations, with clonal selection and horticultural management, potentially shifting average annual production by order of magnitude.

Table 12.1: *Predominant propagation method, age distribution and spatial distribution of fruit trees in different cropping systems: modified from (Verheij and Coronel 1992).*

Cropping system	Propagules	Tree ages	Tree spacing	Number of tree species	Market value chains
I. Collecting wild fruit	Seed	'Random'	'Random'	Very high	Opportunistic, multi-step
II. Fruit-enriched fallows and agroforests	Seed	Even	Clustered	Very high	Opportunistic, multi-step
III. Home gardens	Seed/clonal	Uneven	Uneven	High	Opportunistic, multi-step
IV. Orchards	Clonal	Even	Even	Fewer	Organised, multi-step
V. Corporate plantations	Clonal	Even	Even	Few ^A	Organised, vertical integration

^A With apple, citrus, and the non-tree perennials pineapple and banana's as global leaders (in coconut, cashew, cacao and coffee interest is in the seed rather than the fruit)

These five stages of cropping/collection systems have coexisted in many parts of the world for a considerable length of time, as transitions towards the 'orchard' mode of specialised production require complex processes of domestication alongside reorganisation of rural-urban markets, in which past success with a few species is not easily replicated with others.

Specialised disciplines in horticulture and pomology refer to the home gardens ('hortus') and specific fruit types ('pomus' or apple) as targets. A more comprehensive multistage tree domestication concept has gradually emerged, and it tends to have fruit trees on the I-II or II-III transitions as a favoured topic. However, the co-evolution of market supply and demand is as challenging as the increased human control over tree growth, phenology, chemical defence, taste and smell attractants, and fruit/seed ratios. These are quite responsive to genetic selection and tree management, and perishability or 'shelf life' of the fruits. New ways of fruit preservation (jams, jellies, sun-dried fruit, freeze-dried fruit, cold storage of pulp for juice blending) are often essential to stabilise farmgate prices.

Concentrations of fruit trees in 'natural' forests in the Amazon have been attributed to past human settlements (Posey 1985, Denevan 1992), like has also been documented for Southeast Asia (Tata et al 2008, van Noordwijk et al 2012). Here, the temporary shelters built by farmers in 'swiddens' became the source of many local fruit trees farmers like to eat – coming back to the patch long after the swidden has transformed into a fallow/forest vegetation. Similar reports have been reported from Africa (Fairhead and Leach 1996). In the humid forest zone of Madagascar, fruit-eating lemur species are the main tree seed dispersal agents, crucial for successful regeneration of forest vegetation. A total of 150 wild fruit species (82 genera, 42 families) are collected from the forest as human diets. For a few species, local tree domestication has been initiated by managing naturally established species or planting in agricultural fields (Styger et al 1999). West African cocoa agroforests may be similar. On 21 ha of cocoa agroforests surveyed in Nigeria, 487 non-cocoa trees belonging to 45 species and 24 families were encountered, with 87% of the trees having edible fruits (Oke and Odebiyi 2007). Similar tree diversity on cocoa farms was found in Ivory Coast (Dumont et al 2014). In surveys in Cameroon and Nigeria, smaller farms were found to have higher fruit tree densities, a relationship that was particularly strong in communities with good market access (Degrande et al 2006). A recent study on the consequences of the 'open access' for community members to fruit trees in cacao agroforestry systems in Cameroon suggested that change of tenure rules may be needed to achieve a more balanced incentive for maintaining, or even increasing fruit tree presence in such systems from the farmers' perspective (Folefack and Darr 2021).

Farmer's choice for trees in cocoa agroforestry systems tends to be gender-differentiated, with fruit trees higher on the women's than on the men's preference lists (Sari et al 2020), suggesting balanced gender relations support tree diversity. In the coffee-growing landscapes of the Yayu biosphere reserve in Ethiopia, nutritional security was highest for households that had access to forests, home gardens and other agroforestry plots beyond market-based coffee income (Jemal et al 2018). Tree diversity on and around the farm is crucial for a sustainable agroforestry (AF) system. Fruit properties, such as taste, fruit size, colour and seasonality, were important for acceptability at the local market level in Western Africa (Dawson et al 2012). Wider

acceptance of fruit tree species is highly dependent on successful mass production using year-round propagation techniques that don't depend on availability of fresh seeds. Thus, species for which vegetative propagation can be easily upscaled, tend to get more representation on AF farms (Leakey 2012). The propagation methods used for fruit tree multiplication and upscaling are diverse (Table 12.2). Agroforestry systems such as cocoa, coffee, and home gardens had a higher number of fruit species, especially indigenous ones, compared to crops of other uses (Degrande et al 2006). A substantial share of indigenous fruit trees is either in the 'retained' (preceding current land use) or 'tolerated' (managed volunteer trees), rather than the 'planted' category (Ordonez et al 2014), but systematic data on such distinctions are not available.

Table 12.2: Vegetative propagation techniques used and found appropriate for different fruit tree species (Tchoundjeu et al 2008)

Species	Option 1	Option2	Option 3
<i>Irvingia gabonensis</i>	Top cleft grafting (60%)	Rooting of cutting (50%)	/
<i>Dacryodes edulis</i>	Marcotting (60%)	Rooting of cutting (70%)	/
<i>Ricinodendron heudelotii</i>	Top-cleft grafting (70%)	Marcotting (60%)	Rooting of cuttings (50%)
<i>Cola nitida</i>	Side-tongue grafting (60%)	Rooting of cutting (30%)	Marcotting (30%)
<i>Citrus</i> spp.	Budding (80%)	Marcotting (50%)	Rooting of cutting (50%)
<i>Persea americana</i>	Side-tongue grafting (75%)	/	/
<i>Mangifera indica</i>	Side-tongue grafting (75%)	Marcotting (60%)	/
<i>Garcinia kola</i>	Side-tongue grafting (80%)	/	/
<i>Psidium guajava</i>	Marcotting (90%)	/	/
<i>Theobroma cacao</i>	Top-cleft grafting (80%)	Rooting of cutting (70%)	Marcotting (60%)
<i>Gnetum africanum</i>	Rooting of cutting (60%)	/	/

5. Tree biological challenges to domestication

Most of Africa's indigenous fruit trees remain at the bottom of the domestication and improvement trajectory, where their cultivation primarily depends on unimproved, local, and suboptimal planting material. Moreover, they face challenges of competition from imported non-indigenous fruits and a general lack of climate-suitable, market-acceptable, and on-farm adaptable germplasm. Having these properties hard-wired into indigenous trees can bolster fruit production at local and regional levels that can boost the economy, enhance the population's nutritional status, and contribute to greener and cleaner agricultural production systems.

Fruit tree domestication and cultivation came after the establishment of grain agriculture, probably six to eight millennia ago (Spiegel-Roy 1986, Janick 2005), especially for perennial tree and non-tree species with easy vegetative propagation (grape, olive, date, fig, banana) or polyembryony (citrus, mango). The tree biological traits that discouraged animals from specialising in seed predation through uneven and unpredictable production, short periods of ripeness and modest fruit/seed energy investment ratios are major challenges for the emergence of specialised farming systems that have fruits as more than an opportunistic add-on. For only a very limited number of fruits have the domestication barriers been overcome (Simons and Leakey 2004) – and for those where storage and perishability issues were resolved, globally competitive markets emerged. Meanwhile, urban consumers have access to imported fruit (apples, citrus) even when a huge diversity of local fruits of similar or superior quality lingers away in the forest edge and countryside, without effective access to markets.

Several physiological challenges are to be overcome before a regular and predictable fruit yield is achievable, rather than a boom and bust cycle of overproduction and missed production years (Smith and Samach 2013). The low predictability tree phenology in flowering and fruiting has been discussed since the early days of agroforestry research (Huxley 1996, 1999), but progress has been limited (van Noordwijk et al 2019).

As a model species of farmer-led, research-participatory domestication research, the domestication of *Irvingia gabonensis* (bush mango), a fruit tree grown in agroforestry systems in West and Central Africa, can serve as an example of the challenges to be overcome. The tree has wide phenotypic variation in fruit, nut and kernel traits. Significant differences between recently planted and naturally established trees indicate scope for enhancing the nutritional and economic security of subsistence farmers in the region and a need to conserve natural genetic diversity (Anegbeh et al 2003). Variation in regularity of fruit production is harder to quantify than that in fruit properties. One has to hope that selection for high-yielding trees doesn't imply a selection for higher temporal variability and sensitivity to stress in environments beyond those where selection occurred.

A participatory approach to tree domestication now supplements the more traditional aspects of tree improvement (Leakey et al 2005, Jamnadas et al 2019), with consequences for how 'priority setting' questions are approached (Franzel et al 2008). In the southern Africa region, indigenous fruit trees such as *Uapaca kirkiana*, *Ziziphus mauritiana*, *Adansonia digitata* and *Sclerocarya birrea* are widely preferred by farmers and traded. Domestication of these fruit tree species has advanced and superior clones with multiple traits identified, tested, and disseminated to farmers (Akinnifesi et al 2008). A source of inspiration could be the diversity-oriented fruit tree processing cooperative initiated in Para state in Brazil by farmers

with Japanese roots and a strong market-oriented, diversity-based orientation in agroforestry (Smith et al 1996), processing a wide range of fruits when they are in season, for extracts with domestic ice-cream and overseas markets (Saes et al 2014).

Fruit tree production system needs a functional ecosystem of various facets of domestication (Figure 12.1), recommended practice of tree husbandry and cultivation practices, access and supply of improved germplasm in a socioeconomic context. Among the challenges and opportunities to mainstream and improve ‘orphan crops’ including fruit trees (Dawson et al 2019), traits such as early production, synchronised bearing, tree architecture, ease of harvesting, less labour intensive processing, shelf-life and tolerance of transport come on top of traditional targets like yield, taste, acceptability and stress tolerance. Using exemplars from established crops with a long domestication and improvement history, it is proposed how the modern tools and methods can be incorporated in designing improvement processes for the perennial fruit crops. Having reliable propagation techniques is an important impediment in commercialising and upscaling perennial fruit tree production systems. Mass production of trait-improved germplasm is needed to reach the many farmers who can benefit. In agroforestry fruit species, ICRAF-proposed participatory domestication using farmer’s knowledge and experience is an important component for orphan crop selection.

Using modern genomics tools, the lagging basal pre-breeding curve and lengthy breeding trajectory for genetic gains can be achieved with one-third of the time needed for traditional improvement (Hickey et al 2017). A fine balance between domestication, improvement and productive diversity can be achieved by using various options based on traditional and modern methods of crop improvement. Most of the underutilized tree crops range between undomesticated natural forms (foraged from forests such as *Sclerocarya birrea*, *Allanblackia*, *Butyrospermum* etc.) to a few clonally propagated special purpose trees with pockets of production excellence (e.g. mango, avocado, grapes etc.). A conceptual scheme was proposed by Dawson et al (2019) to tame this tree species’ heterogeneity to make them more adaptable, scalable, with modern technologies (Figure 12.1). The political and societal debate on which techniques, beyond trait-based selection, as accepted as ways to modify the genetic make-up of species (Dalla Costa et al 2017), with specific concerns for all parts of existing value chains that may have to document that they are not involved in such techniques, as soon as modified planting material becomes available.

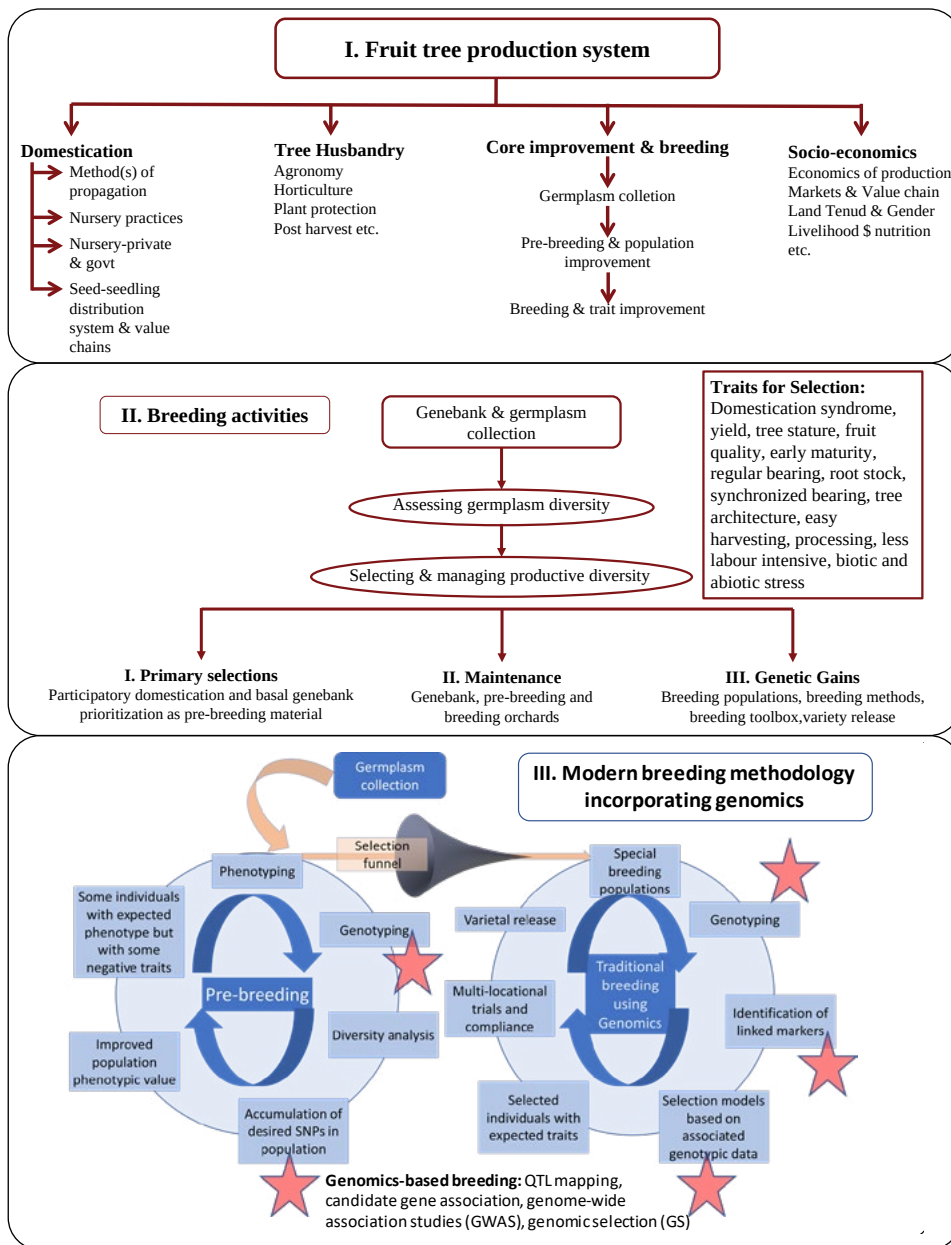


Figure 12.1: Three layers of modernised fruit tree production system driven by genetics, breeding and improvement and genomics. I. describes various elements of fruit tree production system viz. domestication, tree husbandry, improvement & breeding, and socioeconomics. II. describes flow chart and various elements of breeding and improvement activities, III. describes modernised breeding methodology incorporated with genomics-based methods, the boxes marked with “star” are the overlayers entry points for genomics in the traditional breeding pipelines (SNP = single-nucleotide polymorphism; QTL = quantitative trait locus)

6. Building blocks for targeted research and development

From this brief exploration, we derive the following building blocks for a targeted research and development effort to reduce fruit-consumption deficits in Africa and selective parts of Asia:

Compared to grain, pulses and tubers, the human utilisation of fruits faces considerable challenges in overcoming deeply encoded plant strategies that tend to make fruit production erratic with short shelf lives. Research and development efforts have to overcome simultaneous hurdles on the biological and marketing side, with processing and storage techniques (pomology), farmgate – end-user value chains and horticultural management interacting with genetic properties and opportunities for vegetative (clonal) reproduction of selected germplasm. Biological domestication efforts need to be fully embedded in market development and processing efforts, with a clear perspective on the interests of farmer-producers and end-users.

To support mainstreaming and future scaling of their use, research interests and investments should focus on filling data gaps on food composition of indigenous fruit tree species. This would enable the selection of nutrient-rich species for domestication programmes and their wider use in future food systems (Jemal et al 2021). While also supporting their inclusion and promotion in national food-based dietary guidelines, which provide a context-specific basis for public food and nutrition, health and agricultural policies and nutrition education programmes to foster healthier diets. On the demand side, programs to induce positive behavioural change for increasing fruit consumption will need to align to social and cultural contexts, while processing, packaging and marketing needs to account for preferences and expectations of people across age, gender and social groupings (McMullin et al 2021). It is inherent to the fruit tree- dispersal agent syndrome that short-lived excesses in production goes hand in hand with consumption deficits for most of the year or close by excess supply; the access-excess buffer zone is small (van Noordwijk and Cadisch 2002). Fruit tree processing and marketing require different paradigms than plant products of lower perishability and more predictable production properties. Portfolio management of tree diversity rather than specialised monocultures can work both at the household and marketing/processing level.

Compared to grain, pulses and tubers, in fruit trees as different category, modes of production (from collecting in the wild to highly organised corporate plantations) coexist over a much wider range of economic development stages; the current success of global trade in a few species with stages IV and V production modes (Table 12.1) in penetrating urban markets in developing countries with substantial underutilised Stage I-III resources, requires integrated economic, social and biological –technical efforts to understand and redress.

There is a large number of underutilised biological fruit tree resources and a considerable research and development investment barrier that needs to be overcome before small-scale private investors can take things forward. The associated collective action deficit is further

increased by countries restrictive *Intellectual Property Rights* policies and expectations of pay-offs on the intrinsic value of ‘their’ biological diversity, which generally does not recognise borders that coincide with nation-states.

Yet, the few fruit trees that made it to international trade value chains are considerable sources of income and contributors to healthy diets, especially as they can be stored in cold places, harvested before they are ripe and ripened under controlled conditions. The production systems classification of Table 12.1 can be used for cross-continental lessons learnt on success and failure that involve the biological properties of fruits and trees, the technical processing and economic value chains between fruit tree, farmgate and end-user, and the shifting perspectives and priorities of urban consumers, influenced by marketing and promotional campaigns. Existing data on fruit production, export and import for Africa as a whole suggests that few fruit trees native to Africa are major income sources (Table 12.3).

Table 12.3: Fruit tree production, exports from and imports to African countries in 2019.

Item	Area (M ha)	Quantity, M			Value, Billion US\$		
		Production	Export	Import	Export	Import	Net
Citrus (oranges, grapefruit, tangerines, etc.)	1.70	19.33	4.54	0.22	2.46	0.16	2.30
Cashew nuts + apple	4.77	2.58	1.73	0.01	1.97	0.05	1.92
Grapes	0.34	4.89	0.51	0.05	0.82	0.07	0.75
Olives	3.41	4.88	0.35	0.06	0.78	0.13	0.64
Fruits (various)	1.22	7.01	1.04	0.24	0.89	0.27	0.60
Nuts (various)	0.16	0.23	0.10	0.05	0.59	0.18	0.41
Avocados	0.12	0.95	0.16	0.02	0.25	0.02	0.24
Bananas	1.88	21.48	0.85	0.50	0.42	0.22	0.20
Dates	0.44	3.83	0.21	0.18	0.42	0.24	0.17
Mangoes, mangosteens, guavas	1.04	8.956	0.10	0.02	0.15	0.01	0.14
Pears	0.04	0.75	0.24	0.08	0.19	0.07	0.12
Karite nuts (sheanuts)	0.84	0.76	0.23	0.0003	0.11	0	0.11
Plums, Apricots, Peaches and nectarines	0.19	1.98	0.08	0.05	0.11	0.08	0.03
Plantains and others	4.42	26.71	0.11	0.09	0.033	0.03	0.007
Kola nuts	0.63	0.31	0.03	0.02	0.006	0.003	0.003
Papayas	0.15	1.48	0.01	0.01	0.005	0.003	0.002
Coconuts	1.16	1.86	0.08	0.10	0.02	0.05	(0.03)
Almonds	0.52	0.30	0.003	0.02	0.01	0.15	(0.14)
Apples	0.16	3.13	0.49	0.58	0.39	0.70	(0.30)

Source: FAOstat

In the absence of comprehensive analysis, quantitative targets for increasing production and reducing consumption deficits are probably ill-advised. However, retaining fruit tree diversity as part of market-based production of cocoa, coffee, rubber, palm oil, or cashew is probably a risk-reducing strategy.

The African orphan crops consortium (Hendre et al 2019, AOCC 2020), a public-private partnership hosted by World Agroforestry (CIFOR-ICRAF), is heavily investing in research and development activities for its mandated 101 crops (including around 50 fruit tree crops) by developing genomics resources (Jamnadass et al 2020) to aid in improvement and breeding and also by training 150 African plant breeders to use these tools in their breeding programs. Apart from the core research and development agenda, a sustainable, long-term, and self-reliant fruit-production system needs strong partnerships between international and national organisations. This is necessary to bring together the inter-disciplinary expertise for developing interdependent production, marketing, and processing technologies to feed into local-, country-, regional-, and global-level cyclical agro-economy.

References

- Akinnifesi FK, Sileshi G, Ajayi OC, Chirwa PW, Kwesiga FR, Harawa R. 2008. Contributions of agroforestry research and development to livelihood of smallholder farmers in Southern Africa: 2. Fruit, medicinal, fuelwood and fodder tree systems. *Agricultural Journal* 3(1):76–88.
- Anegbeh PO, Usoro C, Ukafor V, Tchoundjeu Z, Leakey RRB, Schreckenberk K. 2003. Domestication of *Irvingia gabonensis*: 3. Phenotypic variation of fruits and kernels in a Nigerian village. *Agroforestry systems* 58(3):213–218.
- [AOCC] African Orphan Crops Consortium. 2020. <http://africanorphancrops.org/>
- Bharucha Z, Pretty J. 2010. The roles and values of wild foods in agricultural systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1554):2913–2926.
- Coulibaly-Lingani P, Tigabu M, Savadogo P, Oden PC, Ouadba JM. 2009. Determinants of access to forest products in southern Burkina Faso. *Forest policy and economics* 11(7):516–524.
- Dalla Costa L, Malnoy M, Gribaudo I. 2017. Breeding next generation tree fruits: technical and legal challenges. *Horticulture research* 4(1):1–11.
- Dawson I, Harwood C, Jamnadass R, Beniast J, eds. 2012. *Agroforestry tree domestication: a primer*. Nairobi, Kenya: World Agroforestry Centre. 148 pp
- Dawson IK, Powell W, Sila D, Simons T, Revoredo-Giha C, Odeny DA, Barnes A P, Watson CA, Hoard S, Burnett F, Hale IL, Van Deynze A, Mayes S, Kindt R , Cheng S, Xu X, Guarino L, Shapiro H, Jamnadass R, Prabhu R, Graudal L, McMullin S, Muchugi A, Hendre P, Roshetko JM. 2018. *Supporting human nutrition in Africa through the integration of new and orphan crops into food systems: placing the work of the African Orphan Crops Consortium in context*. ICRAF Working Paper 276. Nairobi, Kenya: World Agroforestry Centre. DOI: <http://dx.doi.org/10.5716/WP18003.PDF>

- Dawson IK, Powell W, Hendre PS, Bancic J, Hickey J, Kindt R, Hoad S, Hale I, Jamnadass R. 2019. Mainstreaming the production of new and orphan crops to diversify food systems and support human nutrition: exploring production trends, defining crop development objectives and determining breeding approaches. *New Phytologist* 224:37–54. doi: 10.1111/nph.15895.
- Degrande A, Schreckenber K, Mbosso C, Anegbeh P, Okafor V, Kanmegne J. 2006. Farmers' fruit tree-growing strategies in the humid forest zone of Cameroon and Nigeria. *Agroforestry Systems* 67(2): 159–175.
- Denevan WM. 1992. The pristine myth: the landscape of the Americas in 1492. *Annals of the Association of American Geographers* 82(3):369–385.
- Dumont ES, Gnahoua GM, Ohouo L, Sinclair FL, Vaast P. 2014. Farmers in Côte d'Ivoire value integrating tree diversity in cocoa for the provision of ecosystem services. *Agroforestry systems* 88(6):1047–1066.
- Elmadfa I, Meyer A. 2010. Importance of food composition data to nutrition and public health. *Eur J Clin Nutr* 64:S4–S7. <https://doi.org/10.1038/ejcn.2010.202>
- Fairhead J, Leach M. 1996. Misreading the African landscape: society and ecology in a forest-savanna mosaic (Vol. 90). Cambridge, UK: Cambridge University Press.
- [FAO] Food and Agriculture Organization. 2020. <http://www.fao.org/faostat/en/#home> (Accessed 18th Jun 2020).
- [FDC] FoodData Central. 2020. <https://fdc.nal.usda.gov/> (Accessed 18th June 2020).
- Folefack AJJ, Darr D. 2021. Promoting cocoa agroforestry under conditions of separated ownership of land and trees: strengthening customary tenure institutions in Cameroon. *Land Use Policy* 108:105524.
- Franzel S, Akinnifesi FK, Ham C. 2008. Setting priorities among indigenous fruit tree species in Africa: examples from southern, eastern and western Africa regions. In: *Indigenous fruit trees in the tropics: domestication, utilization and commercialization*. CAB International, Wallingford, UK, in association with the World Agroforestry Centre, Nairobi, Kenya: 1-27.
- Gautier-Hion A, Duplantier JM, Quris R, Feer F, Sourd C, Decoux JP, Dubost G, Emmons L, Erard C, Hecketsweiler P, Mougazi A. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65(3):324–337.
- Goldschmidt EE. 2013. The evolution of fruit tree productivity: a review. *Economic botany* 67(1):51–62.
- GRIN-global. 2020. <https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearcheco.aspx> (Accessed 18th June 2020).
- Harris J, de Steenhuijsen P, PETERS B, McMullin S, Bajwa B, de Jager I, Brouwer ID. 2021. Fruits and vegetables for healthy diets: priorities for food system research and action. Food Systems Summit Brief prepared by Research Partners of the Scientific Group for the Food Systems Summit March, 2021. doi.org/10.48565/scfss2021-ys30.
- Harrison ME, Zweifel N, Husson SJ, Cheyne SM, D'Arcy LJ, Harsanto FA, Morrogh-Bernard HC, Purwanto A, Vogel ER, Wich SA, and Van Noordwijk MA. 2016. Disparity in onset timing and frequency of flowering and fruiting events in two Bornean peat-swamp forests. *Biotropica* 48(2): 188–197.

- Hendre PS, Muthemba S, Kariba R, Muchugi A, Fu Y, Chang Y, Song B, Liu H, Liu M, Liao X, Sahu SK, Wang S, Li L, Lu H, Peng S, Cheng S, Xu X, Yang H, Wang J, Liu X, Simons A, Shapiro HY, Mumm RH, Van Deynze A, Jamnadass R. 2019. African Orphan Crops Consortium (AOCC): status of developing genomic resources for African orphan crops. *Planta* 250:(989–1003). <https://doi.org/10.1007/s00425-019-03156-9>
- Hickey JM, Chiurugwi T, Mackay I, Powell W, Eggen A, Kilian A, Jones C, Canales C, Grattapaglia D, Bassi F, Atlin G. 2017. Genomic prediction unifies animal and plant breeding programs to form platforms for biological discovery. *Nature Genetics* 49:1297–1303, <https://doi.org/10.1038/ng.3920>
- Huxley PA. 1996. Biological factors affecting form and function in woody-non-woody plant mixtures. In: Ong CK, Huxley PA, eds. *Tree crop interactions: a physiological approach*. Wallingford, UK: CAB International; Nairobi, Kenya: World Agroforestry (ICRAF). p.235–298.
- Huxley PA. 1999. *Tropical Agroforestry*. Oxford: Blackwell Science.
- Ickowitz A, Powell B, Salim MA, Sunderland T. 2014. Dietary quality and tree cover in Africa. *Global Environmental Change* 24:287–294.
- Jamnadass RH, Dawson IK, Franzel S, Leakey RRB, Mithöfer D, Akinnifesi FK, Tchoundjeu Z. 2011. Improving livelihoods and nutrition in sub-Saharan Africa through the promotion of indigenous and exotic fruit production in smallholders' agroforestry systems: a review. *International Forestry Review* 13(3):338–354.
- Jamnadass R, Ofori DA, Dawson IK, Tchoundjeu Z, McMullin S, Hendre PS, Graudal L. 2019. Enhancing agroforestry systems through tree domestication. In: van Noordwijk M, ed. *Sustainable development through trees on farms: agroforestry in its fifth decade*. Bogor, Indonesia: World Agroforestry (ICRAF). p.45–59.
- Jamnadass R, Mumm RH, Hale I, Hendre P, Muchugi A, Dawson IK, Powell W, Graudal L, Yana-Shapiro H, Simons AJ, Van Deynze A. 2020. Enhancing African orphan crops with genomics. *Nature Genetics* 52(4):356–360. <https://doi.org/10.1038/s41588-020-0601-x>
- Janick J. 2005. The origins of fruits, fruit growing, and fruit breeding. *Plant breeding reviews* 25:255–320.
- Jemal O, Callo-Concha D, van Noordwijk M. 2018. Local agroforestry practices for food and nutrition security of smallholder farm households in southwestern Ethiopia. *Sustainability* 10(8):2722.
- Jemal OM, Callo-Concha D, van Noordwijk M. 2021. Coffee agroforestry and the food and nutrition security of small farmers of South-Western Ethiopia. *Front. Sustain. Food Syst.* 5:608868. doi: 10.3389/fsufs.2021.608868
- Kenyatta C, Henderson A, eds. 2001. The potential of indigenous wild foods, Workshop Proceedings, 22-26 January 2001. CRS/Southern Sudan. https://fr.fsnnetwork.org/sites/default/files/indigenous_wild_foods.pdf#page=42
- Khoury CK, Amariles D, Soto JS, Diaz MV, Sotelo S, Sosa CC, Ramírez-Villegas J, Achicanoy HA, Velásquez-Tibatá J, Guarino L, León B. 2019. Comprehensiveness of conservation of useful wild plants: an operational indicator for biodiversity and sustainable development targets. *Ecological indicators* 98:420–429.
- Kindt, R. 2020a. WorldFlora: An R package for exact and fuzzy matching of plant names against the World Flora Online taxonomic backbone data. *Applications in Plant Sciences* 8(9):e11388.
- Kindt R. 2020b, Countries and their ISO 3166-1 alpha-3 codes matched to the World geographical scheme for recording plant distributions, <https://doi.org/10.34725/DVN/HLRXNF>, World Agroforestry - Research Data Repository, V2, UNF:6:k6MZ9DCzINruoTNs8zRgmg== (fileUNF)

- Kindt R, Dawson IK, Lillesø J-PB, Muchugi A, Pedercini F, Roshetko J, van Noordwijk M, Graudal L, Jamnadass R 2021. *The one hundred tree species prioritized for planting in the tropics and subtropics as indicated by database mining*. Working Paper No. 312. Nairobi, Kenya: World Agroforestry (ICRAF). . DOI <http://dx.doi.org/10.5716/WP21001.PDF>
- Leakey RR, Tchoundjeu Z, Schreckenberg K, Shackleton SE, Shackleton CM. 2005. Agroforestry tree products (AFTPs): targeting poverty reduction and enhanced livelihoods. *International Journal of Agricultural Sustainability* 3(1):1–23.
- Leakey RRB. 2012. Participatory domestication of indigenous fruit and nut trees: new crops for sustainable agriculture in developing countries. In: Gepts P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, Qualset CO, eds. *Biodiversity in agriculture: domestication, evolution, and sustainability*. Cambridge, UK: Cambridge University Press.
- McMullin S, Njogu K, Wekesa B, Gachui A, Ngethe E, Stadlmayr B, Jamnadass R, Kehlenbeck K. 2019. Developing fruit tree portfolios that link agriculture more effectively with nutrition and health: a new approach for providing year-round micronutrients to smallholder farmers. *Food Security* 11(6):1355–1372.
- McMullin S, Stadlmayr B, Ngethe E, Wekesa B, Njogu K, Gachui A, Mbaya B, Katiwa A, Jamnadass R. 2020. Trees nurture nutrition: an insight on how to integrate locally available food tree and crop species in school gardens. In: Hunter D, Monville-Oro E, Burgos B, Roel CN, Calub B, Gonsalves J, Lauridsen N, eds. *Agrobiodiversity, school gardens and healthy diets. Promoting Biodiversity, Food and Sustainable Nutrition*. Earthscan Routledge.
- McMullin S, Stadlmayr B, Mausch K, Revoredo-Giha C, Burnett F, Guarino L, Brouwer ID, Jamnadass R, Graudal L, Powell W, Dawson IK. 2021. Determining appropriate interventions to mainstream nutritious orphan crops into African food systems. *Global Food Security* 28:100465. doi:10.1016/j.gfs.2020.100465.
- Oke DO, Odebiyi KA. 2007. Traditional cocoa-based agroforestry and forest species conservation in Ondo State, Nigeria. *Agriculture, Ecosystems & Environment* 122(3):305–311.
- Ordóñez JC, Luedeling E, Kindt R, Tata HL, Harja D, Jamnadass R, van Noordwijk M. 2014. Constraints and opportunities for tree diversity management along the forest transition curve to achieve multifunctional agriculture. *Current Opinion in Environmental Sustainability* 6:54–60.
- Posey DA. 1985. Indigenous management of tropical forest ecosystems: the case of the Kayapo Indians of the Brazilian Amazon. *Agroforestry systems* 3(2):139–158.
- Saes MSM, Silva VL, Nunes R, Gomes TM. 2014. Partnerships, learning, and adaptation: a cooperative founded by Japanese immigrants in the Amazon rainforest. *International Journal of Business and Social Science* 5(12):131–141.
- Sari RR, Saputra DD, Hairiah K, Rozendaal D, Roshetko JM, van Noordwijk M. 2020. Gendered species preferences link tree diversity and carbon stocks in Cacao agroforest in Southeast Sulawesi, Indonesia. *Land* 9(4):108.
- Siegel KR, Ali MK, Srinivasiah A, Nugent RA, Narayan KMV. 2014. Do We Produce Enough Fruits and Vegetables to Meet Global Health Need? *PLoS One* 9:e104059. <https://doi.org/10.1371/journal.pone.0104059>.
- Sinnott-Armstrong MA, Downie AE, Federman S, Valido A, Jordano P, Donoghue MJ. 2018. Global geographic patterns in the colours and sizes of animal-dispersed fruits. *Global Ecology and Biogeography* 27(11):1339–1351.

- Spiegel-Roy P. 1986. Domestication of fruit trees. *Developments in Agricultural and Managed Forest Ecology* 16:201–211.
- Stadlmayr B, Charrondi re UR, Eisenwagen S, Jamnadass R, Kehlenbeck K. 2013. Nutrient composition of selected indigenous fruits from sub-Saharan Africa. *Journal of the Science of Food and Agriculture* 93(11):2627–2636
- Stadlmayr B, McMullin S, Innocent J, Kindt R, Jamnadass R. 2019. Priority Food Tree and Crop Food Composition Database: Online database. Version 1. Nairobi, Kenya: World Agroforestry.
- Styger E, Rakotoarimanana JEM, Rabevohitra R, Fernandes ECM. 1999. Indigenous fruit trees of Madagascar: potential components of agroforestry systems to improve human nutrition and restore biological diversity. *Agroforestry systems* 46(3):289–310.
- Simons AJ, Leakey RRB. 2004. Tree domestication in tropical agroforestry. *Agroforestry Systems* 61: 167–181.
- Smith HM, Samach A. 2013. Constraints to obtaining consistent annual yields in perennial tree crops. I: Heavy fruit load dominates over vegetative growth. *Plant Science* 207:158–167.
- Smith NJ, Falesi IC, Alvim PDT, Serr o EAS. 1996. Agroforestry trajectories among smallholders in the Brazilian Amazon: innovation and resiliency in pioneer and older settled areas. *Ecological economics* 18(1):15–27.
- Tata HL, van Noordwijk M, Werger M. 2008. Trees and regeneration in rubber agroforests and other forest-derived vegetation in Jambi (Sumatra, Indonesia). *Journal of Forestry Research* 5(1):1–20.
- Tchoundjeu Z, Atangana A, Asaah E, Tsoheng A, Facheux C, Foundjem D, Mbosso C, Degrande A, Sado T, Kanmegne J, Mbile P, Tabuna H, Anegbeh P, Useni M. 2008. Domestication, Utilization and Marketing of Indigenous Fruit Trees in West and Central Africa. In: Akinnifesi FK, Leakey RRB, Ajayi OO, Sileshi G, Tchoundjeu Z, Matakala P, Kwesiga FR, eds. *Indigenous fruit tree in the tropics: domestication, utilization and commercialization*. Wallingford, UK: CAB International. p.171–183.
- van Noordwijk M. 1984. *Ecology textbook for the Sudan*. Amsterdam, Netherlands: Ecologische Uitgeverij; Khartoum, Sudan: Khartoum University Press. <http://apps.worldagroforestry.org/region/sea/publications/detail?pubID=1052>
- van Noordwijk M, Cadisch G. 2002. Access and excess problems in plant nutrition. *Plant and Soil* 247: 25–39.
- van Noordwijk M, Tata HL, Xu J, Dewi S, Minang PA. 2012. Segregate or integrate for multifunctionality and sustained change through rubber-based agroforestry in Indonesia and China. In: Nair P, Garrity D, eds. *Agroforestry-the future of global land use*. Dordrecht, Netherlands: Springer. p.69–104.
- van Noordwijk M, Bizard V, Wangpakapattanawong P, Tata HL, Villamor GB, Leimona B. 2014. Tree cover transitions and food security in Southeast Asia. *Global Food Security* 3(3–4):200–208.
- van Noordwijk M, Rahayu S, Gebrekirstos A, Kindt R, Tata HL, Muchugi A, Ordonnez JC, Xu J. 2019. Tree diversity as basis of agroforestry. In: van Noordwijk M, ed. *Sustainable development through trees on farms: agroforestry in its fifth decade*. Bogor, Indonesia: World Agroforestry (ICRAF). p.17–43.
- van Zonneveld M, Kindt R, Solberg S , N’Danikou S, Dawson IK. 2020. Diversity and conservation of traditional African vegetables: priorities for action. *Divers Distrib* 27(2):216–232. <https://doi.org/10.1111/ddi.13188>

- van Zonneveld M, Volk GM, Dulloo ME, Kindt R, Mayes S, Quintero M, Choudhury D, Achigan-Dako EG, Guarino L. 2021. Safeguarding and using fruit and vegetable biodiversity. Food Systems Summit Brief prepared by Research Partners of the Scientific Group for the Food Systems Summit April 2021. Bonn, Germany: Center for Development Research (ZEF) in cooperation with the Scientific Group for the UN Food System Summit 2021. <https://hdl.handle.net/20.500.11811/9141>
- Verheij EWM, Coronel RE, eds. 1992. *Plant resources of South-East Asia: edible fruits and nuts*. Bogor, Indonesia: Prosea Foundation.
- Vira B, Agarwal B, Jamnadass R, Kleinschmit D, McMullin S, Mansourian S, Neufeldt H, Parrotta JA, Sunderland T, Wildburger C. 2015. Introduction: forests, trees and landscapes for food security and nutrition. In: Vira B, Wildburger C, Mansourian S, eds. *Forests, Trees and Landscapes for Food Security and Nutrition. A Global Assessment Report*. p.14–23.
- [WFO] World Flora Online. 2020. *World Flora Online*. <http://www.worldfloraonline.org> (Accessed 18th June 2020).
- Wheelwright NT, Orians GH. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *The American Naturalist* 119(3):402–413.
- [WGSRPD] World Geographical Scheme for Recording Plant Distributions. <http://www.tdwg.org/standards/109> (Accessed 18th June 2020).
- Zerega NJ, Ragone D, Motley TJ. 2004. Complex origins of breadfruit (*Artocarpus altilis*, *Moraceae*): implications for human migrations in Oceania. *American journal of botany* 91(5):760–766.

