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The role of orphan crops in the transition to nutritional quality-oriented crop improvement

Vincent Verbeecke[1,2], Laura Custódio[1,2], Simon Strobbe[1] and Dominique Van Der Straeten[1,*]

1-Laboratory of Functional Plant Biology, Department of Biology, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium.

2-These authors contributed to the work equally.

[*]Author for correspondence: Dominique.VanDerStraeten@UGent.be

Abstract

Micronutrient malnutrition is a persisting problem threatening global human health. Biofortification via metabolic engineering has been proposed as a cost-effective and short-term means to alleviate this burden. There has been a recent rise in the recognition of potential that underutilized, orphan crops can hold in decreasing malnutrition concerns. Here, we illustrate how orphan crops can serve as a medium to provide micronutrients to populations in need, whilst promoting and maintaining dietary diversity. We provide a roadmap, illustrating which aspects to be taken into consideration when evaluating orphan crops. Recent developments have shown successful biofortification via metabolic engineering in staple crops. This review provides guidance in the implementation of these successes to relevant orphan crop species, with a specific focus on the relevant micronutrients iron, zinc, provitamin A and folates.

Keywords: Micronutrient malnutrition, Biofortification, Orphan crops, Iron, Zinc, Provitamin A, Folates

Highlights

- Micronutrient malnutrition is a persisting global public health problem, particularly affecting poor rural populations.
- Recent developments in biofortification demonstrate that a shift towards nutritional quality improvement in highly consumed crops can alleviate this problem.
- Orphan crops can play a prominent role in feeding specific regional populations, typically burdened by several micronutrient deficiencies.
- Translation of validated biofortification approaches to a variety of orphan crops can be a tremendous asset in the fight against hidden hunger.
- Guidance is provided towards orphan crop biofortification, focusing on iron/zinc, provitamin A and folates.

The global problem of hidden hunger

Malnutrition is a problem that affects more than 2 billion people worldwide (Lowe 2021). The predominant cause for malnutrition is a lack of access to nutritious food (Muthayya 2013; Research Institute (IFPRI) 2014). Micronutrient deficiencies (MNDs) are characterized by an insufficient intake and/or absorption of vitamins and minerals. This often goes unnoticed at the onset, since it initially is manifested in mild to moderate symptoms, and only becomes visible when the deficiency status becomes severe. For this reason, this condition is regarded as "hidden hunger". It is widespread, affecting almost one in every three humans (Muthayya 2013; Ruel-Bergeron 2015). The most affected groups are women at reproductive age and young children, yet MNDs can impair human health at any moment regardless of gender and/or age group (Muthayya 2013).

The overwhelming majority of people affected by MNDs come from lower-income households (Darnton-Hill and Mkparu 2015). People in such conditions most often cannot afford to consume a varied and nutrient-rich diet, such as animal-derived products or fruits and vegetables (Chaudhary, Gustafson, and Mathys 2018). Hence, these diets amount to the occurrence of multiple MNDs in a more frequent way than single MNDs (Darnton-Hill 2012). In other words, MND's often do not come alone, making the issue even more problematic. Currently, among the most pressing micronutrient deficiencies within the general population are iron, zinc and iodine, as well as vitamins A and B9 (folate) (Van Der Straeten 2020; Lowe 2021). Countries that have large shares of the population affected by this condition have a direct negative impact in their economic development given that MNDs can severely reduce cognitive function as well as physical performance (Darnton-Hill 2005; Steur 2012; 2015; Win 2016). The associated long-term health impacts are typically felt by the most vulnerable people in a society, particularly the rural poor and marginalized (Muthayya 2013; Research Institute (IFPRI) 2014).

At first glance, the problem of undernutrition seems a paradox, as we are living in a time of high agricultural productivity. Attaining adequate nutrition, however, is far more complicated than just having access to food to satisfy hunger. Hidden hunger is often the result of monotonous diets that rely heavily on starchy staple crops, such as maize (*Zea mays*), wheat (*Triticum aestivum)* and rice (*Oryza sativa*) (Burchi, Fanzo, and Frison 2011). These provide a high share of daily caloric needs (McKevith 2004), yet often fail to supply adequate amounts of micronutrients (Ruel-Bergeron 2015; S. Strobbe and Van Der Straeten 2018; Titcomb and Tanumihardjo 2019). It is well established that crop breeding has traditionally focused on maximizing yield-associated traits, at the cost of significant genetic diversity (Flint-Garcia 2013; Gillespie and van den Bold 2017). This has resulted in neglect of crop nutritional quality and biodiversity, which negatively impacts human health. Indeed, across different regions and populations dietary diversity was found to positively correlate with nutrient adequacy scores (Nair, Augustine, and Konapur 2016). Additionally, MNDs can be the result of inadequate absorption of micronutrients, which can have a genetic basis or be the result of repetitive exposure to infection and/or inflammation (Bailey, West Jr., and Black 2015). Yet, most agriculture-based solutions haven't focused on nutritional quality gains, as it had been previously understood that malnutrition was simply a consequence of insufficient food production (Thompson, Cohen, and Meerman 2012; El Bilali 2019). It is now clear that tackling malnutrition will require a reform of the current global food system (Branca et al. 2020). This holistic and systematic change will have to be driven through advances in agricultural research and science-based policy making (Pinstrup-Andersen 2007). The current approaches to achieve food and nutrition security include both crop diversification and biofortification (McMullin 2021). These approaches are inherently complementary as they aim to increase the diversity of available foods, whilst also focusing on making them more nutritious (N. Kumar, Harris, and Rawat 2015; de Brauw et al. 2018). In this sense, the inclusion and promotion of orphan crops for consumption, and as an object of biofortification efforts can be an effective path to combat malnutrition (Mabhaudhi 2019; Jamnadass 2020).

The necessity for scientific and agricultural development on orphan crops

Orphan crops (or minor crops) can be described as underutilized crop species that exhibit the following characteristics: they are not (or only limited) the object of research and development; they have marginal to low importance in global food production systems; they are often part of ancient cultural traditions; and they have emergent value due to their unrecognized traits (Gregory 2019; Tadele 2019). These minor crops are almost exclusively produced by small-scale farmers, and they represent a technological opportunity for innovation as they have diverse nutrition profiles. Furthermore, many have been utilized as medicinal plants, which points to their overall benefits for human health (Kamenya et al. 2021). Recently, many orphan crops have been marketed as healthy foods, or superfoods, as was the case for quinoa (*Chenopodium quinoa*). This increase in market interest might represent a shift in perception and the transition from marginal crop to a more widely consumed crop (Assogbadjo et al. 2021).

Orphan crops encompass e.g., cereal, root, fruit, and vegetable crops. These underutilized plant species hold an important role in the support of food security and agriculture in rural locations worldwide (Jamnadass 2020). Enset (*Ensete ventricosum*) for instance is crucial in preventing hunger in Ethiopia by its function as a subsistence crop (Mccabe 1990), meaning that it serves as a food source for the farmers and thus the local community. As such, it stands to reason that they are an important part of any attempt to transform diets and agro-ecosystems. Targeting these orphan crops in future nutrition-focused policies seems favorable, especially because they are already positively viewed and enjoyed by local populations. Traditionally, these have been grown by marginal farmers mainly because they serve as subsistence crops. This means that the primary drive for their cultivation is directly related to survival of a small number of people (Bisht 2014), resulting in a lack of coordinated efforts to improve their productivity, reflected by their low yields. Most orphan crops have been cultivated in unfavorable conditions, which has promoted an enhanced overall resilience and tolerance for varied stress conditions due to evolutionary pressure (Mabhaudhi 2019; Kamenya et al. 2021). Additionally, in comparison to typical staples, these orphan crops were not the object of extensive breeding, being beneficial for the witnessed genetic diversity as well as micronutrient composition in most of them (Burchi, Fanzo, and Frison 2011).

There is a diverse array of underutilized crops that can have a clearly beneficial effect in tackling malnutrition. Yet, the genetic improvement of these crops has been lagging, despite their immense potential and cost-effectiveness(Steur 2010; 2012; 2015; Steur et al. 2017). Below, we illustrate the notion that extending current metabolic engineering approaches to orphan crops can serve to reduce MNDs. We focus on iron, zinc, provitamin A (carotenoids) and folates, as these are micronutrients for which deficiencies are widespread and have been successfully addressed in staple crops.

The role of genetic engineering for crop improvement

Biofortification, an intervention which involves increasing the natural micronutrient content of crops, has been presented as a cost-effective, sustainable method to help eradicate micronutrient deficiencies (Howarth E. Bouis and Saltzman 2017; Hay 2017; Garg 2018; Van Der Straeten 2020). Biofortified crops, obtained via breeding, particularly as part of the Harvest Plus initiative (CAST 2020), have already shown a beneficial impact on micronutrient intake and thus the health of the populations consuming them (Bouis and Saltzman 2017; Garg 2018; Birol and Bouis 2023). Next to breeding, biofortification of crops can be achieved via genetic engineering (GE). Indeed, many efforts have been put into the development of biofortified plants through GE technology over the last decades, and this has mainly been focusing on highly consumed staple crops (Darnton-Hill 2012; Steur 2015; Garg 2018). However, the expected beneficial impact of GE biofortified crops on human health remains in the (very near) future, as the first GE biofortified crop, provitamin A-enriched Golden Rice (Ye and Beyer 1979; Paine 2005; Swamy 2019), was only approved for cultivation in the Philippines in July of 2021. In contrast to GE biofortified crops, biofortification by means of breeding has expanded into orphan crops as well. Examples of these include iron enriched pearl millet (*Pennisetum glaucum*) (K. N. Rai, Govindaraj, and Rao 2012; Finkelstein 2015) and orange-fleshed sweet potato (*Ipomoea batatas*) (Low and Thiele 2020). Biofortification via breeding has the advantage that it suffers less from obstruction by regulation, as compared to GE. GE has the advantage that it is not reliant on adequate genetic variations present in the specific crop and addition of micronutrients can not only go faster but also reach the necessary levels more easily than for regular breeding (Van Der Straeten 2020). If variation is present in the germplasm of a particular crop, meaning that certain sexually compatible accessions depict satisfactory micronutrient levels, breeding could be considered a favorable biofortification method (Van Der Straeten 2020). GE interventions, notwithstanding, hold the potential to tackle multiple (nutritional) target traits at once, thereby tremendously speeding up the process of crop nutritional enhancement (Van Der Straeten 2020). Using genetic engineering for crop improvement also provides the opportunity to incorporate other traits of agronomic interest (Van Der Straeten 2020), such as high-salinity or cold stress tolerance (Rivero et al. 2022). This exemplifies how the choice of breeding, GE or their combination is largely determined by the specific crop-micronutrient(s) combination in mind. This in turn is determined by the targeted population, burdened by one or multiple micronutrient deficiencies, as well as their dietary preferences.

Here, we illustrate the different parameters to be taken into account when considering the use of orphan crops for nutritional quality engineering by scoring 20 orphan crops using radar graphs.

Case study – Tackling micronutrient deficiencies in Western Africa

To introduce a possible mode of action we have chosen Western Africa as an example region. This region has a high prevalence of micronutrient deficiencies (Figure 1) and a considerable diversity of locally consumed orphan crops such as finger millet (*Eleusine coracana*), cassava (*Manihot esculenta,* though often no longer considered an orphan crop), fonio (*Digitaria exilis*), and okra (*Abelmoschus esculentus*). A high percentage of the Western African population strongly suffers from iron, zinc, and/or vitamin A deficiency (Figure 1). Vitamin A deficiency even reaches up to 70% and 75% in Benin and Ghana, respectively. Taking neural tube defect (NTD) prevalence in children under 5 years as a proxy for vitamin B9 deficiency, no severe vitamin B9 insufficiencies seem present in most Western African countries apart from Nigeria (Figure 1). The limited data that exist on exact folate levels in women, however, indicate very high levels of folate deficiency in Sierra Leone (79%), Ghana (53,8%) and Côte d'Ivoire (86%) (Rogers et al. 2018). It is, therefore, reasonable to assume that deficiencies in all four micronutrients are very abundant in Western Africa, though the actual occurrence is subject to intra-national variability.

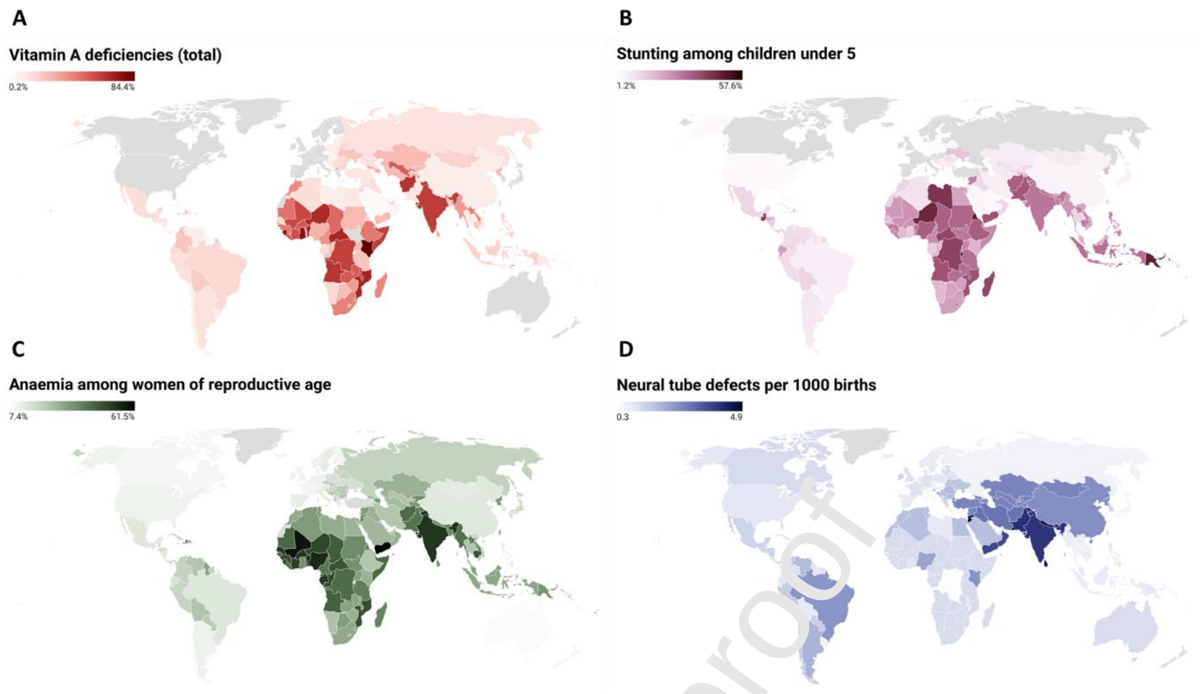

Figure 1: Geographical distribution of micronutrient deficiencies represented through related disease prevalence or micronutrient deficiency itself. A: Prevalence of vitamin A deficiency. Data from WHO, 2005; updated with data from Stevens et al., 2015 (Stevens 2015). B: Zinc deficiency prevalence visualized by stunting among children under five years old (FAO, 2020). Stunting is a common indicator for zinc deficiencies (Stammers 2015). C: Iron deficiency prevalence visualized by anaemia (FAO, 2020). Anaemia is one of the most common symptoms of iron deficiency and iron-deficiency Anaemia (IDA) represents nearly 50% of all anaemia cases (Stoltzfus 2003, Kassebaum 2016). D: Folate deficiency visualized by prevalence of neural tube defects (NTD's) per 1000 births. Folate deficiency is the primary cause of NTD's (The Modell Global Database of Congenital Disorders (Blencowe et al. 2018)). The maps presented here were created with Datawrapper online software.

A list of the most important orphan crops in Western Africa was composed and their nutritional profile was compared with that of important staple crops, including rice, potato, maize, wheat, and sweet potato (Table 1). Next, these crops were divided into four broad categories: fruits/vegetables, roots, cereals and legumes, and scored for nine distinct parameters, namely, crop robustness, yield, biotechnological potential, nutritional completeness, vitamin A content, vitamin B9 content, iron content, zinc content and health benefits. Within each parameter, different factors were utilized in order to score each crop: yield was assessed through crop productivity (in kg per hectare) and estimated post-harvest losses; crop robustness was represented through genetic diversity, breeding potential and stress (both biotic and abiotic) tolerance; biotechnological potential correlated with the availability of a transformation protocol and a genome sequence; nutritional completeness represented 50% of the daily recommended intake in terms of protein, fiber and fat; and, finally, health benefits accounted for the micronutrient density of the crop, the presence of anti-nutritional factors, gluten content, antioxidant content, and proven usage as medicinal plants. This thorough analysis allowed for the construction of the radar graphs presented in figure 2. At a glance, it immediately appears that low yield is a major drawback for all selected orphans, except cassava. Additionally, all orphans score remarkably high on health factors such as high antioxidant content and micronutrient content.

From each category one example crop is taken, for which we addressed which crop-specific interventions are needed to tackle hidden hunger. Broadly speaking, two approaches can be taken. On one hand, biofortification strategies can aim to create more complete crops by enhancing micronutrients that are specifically low in that particular crop. On the other hand, micronutrients that are already acceptably high could be increased to provide enough micronutrients for a person independent of other components of the diet. Millets generally contain acceptable iron levels (Govindaraj et al. 2016; Krishnamurthy et al. 2016; Anitha et al. 2021; Hassan, Sebola, and Mabelebele 2021), but inhabitants of Niger, where millet consumption is high, still suffer from severe iron deficiency anemia, since it is not complemented by other iron rich dietary components (Figure 1). Iron biofortification of millet can thus be advisable. Another example is plantain, for which some cultivars exist that do contain sufficient pro-vitamin A. VAD in regions consuming plantain; however, remains high since these cultivars are not the preferred type for local farmers and consumers (Figure 1, Figure 3) (Norgrove and Hauser 2014). Here as well, breeding programs and GE to develop biofortified plantain could dampen the impact of VAD.

Within the following sections, we will comprehensively discuss specific metabolic engineering strategies for enhancement of micronutrients, as well as current breeding approaches, using plantain, cassava, millets, and cowpea as the chosen examples for the different categories of crops (Figure 4).

Table 1: Daily dietary intake recommendations (DIR, range representative of age and gender specifications) and nutritional content (per 100g of fresh weight) of four staple crops - potato (Solanum tuberosum), rice (Oryza sativa), wheat (Triticum aestivum), maize (Zea mays), soybean (Glycine max) – and twenty-eight orphan crops – Cereals: finger millet (Eleusine coracana), pearl millet (Cenchrus americanus – Penisettum glaucum; monophyletic clade), kodo millet (Paspalum scrobiculatum), teff (Eragrostis tef), Fonio (Digitaria exilis), sorghum (Sorghum bicolor, Sorghum ssp.); fruits: plantain (Musa × paradisiaca), okra (Abelmoschus esculentus); pseudocereals: quinoa (Chenopodium quinoa), amaranth (Amaranthus caudatus L., Amaranthus cruentus L., Amaranthus hypochondriacus L.), buckwheat (Fagopyrum esculentum), chia (Salvia hispanica); root crops: yams (Dioscorea spp., Dioscoreaceae), enset (Ensete ventricosum), cassava (Manihot esculenta), jicama (Pachyrhizus erosus); pulses: chickpea (Cicer arietinum), pigeon pea (Cajanus cajan), grass pea (Lathyrus sativus), cowpea (Vigna unguiculata), Bambara groundnut (Vigna subterranea). All nutritional data corresponds to the amount in 100g of fresh weight (FW) of each crop before any processing or transformation procedure. Sources: USDA (2016). US Department of Agriculture, Agricultural Research Service, Nutrient Data Laboratory. USDA National Nutrient Database for Standard Reference, Release 28. Institute of Medicine. 2006. Dietary Reference Intakes: The Essential Guide to Nutrient Requirements. Washington, DC: The National Academies Press.

	DIR	Potato	Rice	Maize	Wheat	Soybean	Finger millet	Pearl millet	Kodo millet	Teff	Fonio	Sorghum	Plantain	Okra
kcal	2000	77	370	365	327	446	328.00	362	346	367	378	329	122	33
Carbohydrate (g)	60-210	17.5	81.7	74.3	71.2	30.2	72.00	67	59.2	73.1	82.67	72.1	31.9	7.45
Protein (g)	9.1-71	2.05	6.81	9.42	12.61	36.5	7.30	11.7	9.8	13.3	8.5	10.6	1.3	1.93
Vitamin A, RAE (mg)	0.3-1.3	0	0	0.011	0	1	0.00	0.0055	0	0	0	0	0.056	0.036
Vitamin B1 (mg)	0.2-1.4	0.081	0.18	0.385	0.383	0.874	0.48	0.38	0.32	0.39	0.3	0.332	0.062	0.2
Vitamin B6 (mg)	0.1-2.0	0.298	0.107	0.622	0.3	0.377	/	/	/	0.482	/	0.443	0.242	0.215
Vitamin B9 (mg)	0.065-0.6	0.015	0.007	0.019	0.038	0.375	0.02	0.0455	0.0231	0.036	0.0045	0.02	0.022	0.06
Vitamin C (mg)	15-120	19.7	0	0	0	6	0.00	0	0	88	38.5	0	18.4	23
Vitamin E (mg)	4-19	0.01	0	0.49	1.01	0.85	22.00	/	/	0.08	/	0.5	0	0.27
Iron (mg)	0.27-27	0.81	1.6	2.71	3.19	15.7	3.00	8	2.9	7.63	8.48	3.36	0.55	0.62
Zinc (mg)	2-13	0.3	1.2	2.21	2.65	4.89	2.79	3.1	0.7	3.63	3.615	1.67	0.19	0.58
Magnesium (mg)	30-400	23	23	127	126	280	166.35	137	180	184	70	165	36	57
Phosphorous (mg)	100-1250	57	71	210	288	704	229.09	296	188	429	170	289	32	61
Calcium (mg)	200-1300	12	11	7	29	277	281.98	42	27	180	18	13	3	82
Potassium (mg)	400-3400	425	77	287	363	1800	408.00	307	144	427	140	363	487	299

	DIR	Quinoa	Amaranth	Buckwheat	Chia	Ensete	Cassava	Jicama	Chickpea	Pigeon pea	Grass pea	Cowpea	Bambara groundnut
kcal	2000	368	371	343	486	333	160	38	378	343	335	343	335
Carbohydrate (g)	60-210	64.2	65.2	71.5	42.1	64.8	38.1	8.82	63	62.8	50	59.6	65
Protein (g)	9.1-71	14.1	13.6	13.3	16.5	8.3	1.36	0.72	20.5	21.7	27	23.8	20.5
Vitamin A, RAE (mg)	0.3-1.3	0.014	0	0.021	0.054	0	0.001	0.001	0.003	0.001	0.00969	0.002	/
Vitamin B1 (mg)	0.2-1.4	0.36	0.116	0.4	0.62	0.28	0.087	0.02	0.477	0.643	0.46	0.68	0.47
Vitamin B6 (mg)	0.1-2.0	0.47	0.591	0.73	/	/	0.088	0.042	0.535	0.283	0.58	0.361	0.35
Vitamin B9 (mg)	0.065-0.6	0.184	0.082	0.03	0.049	/	0.027	0.012	0.557	0.456	0.54	0.639	0.21
Vitamin C (mg)	15-120	/	4.2	0	1.6	/	20.6	20.2	4	0	5.2	1.5	0.22
Vitamin E (mg)	4-19	2.44	1.19	5.46	0.5	/	0.19	0.46	0.82	0.39	/	/	8.33
Iron (mg)	0.27-27	4.57	7.61	2.2	7.72	8.6	0.27	0.6	4.31	5.23	6.21	9.95	6.5
Zinc (mg)	2-13	3.1	2.87	2.4	4.58	14.1	0.34	0.16	2.76	2.76	4.4	6.11	0.81
Magnesium (mg)	30-400	197	248	231	335	110	21	12	79	183	123	333	7.02
Phosphorous (mg)	100-1250	457	557	347	860	120	27	18	252	367	47	438	308
Calcium (mg)	200-1300	47	159	18	631	130	16	12	57	130	31	85	10.65
Potassium (mg)	400-3400	563	508	460	407	1790	271	150	718	1390	982	1380	1275

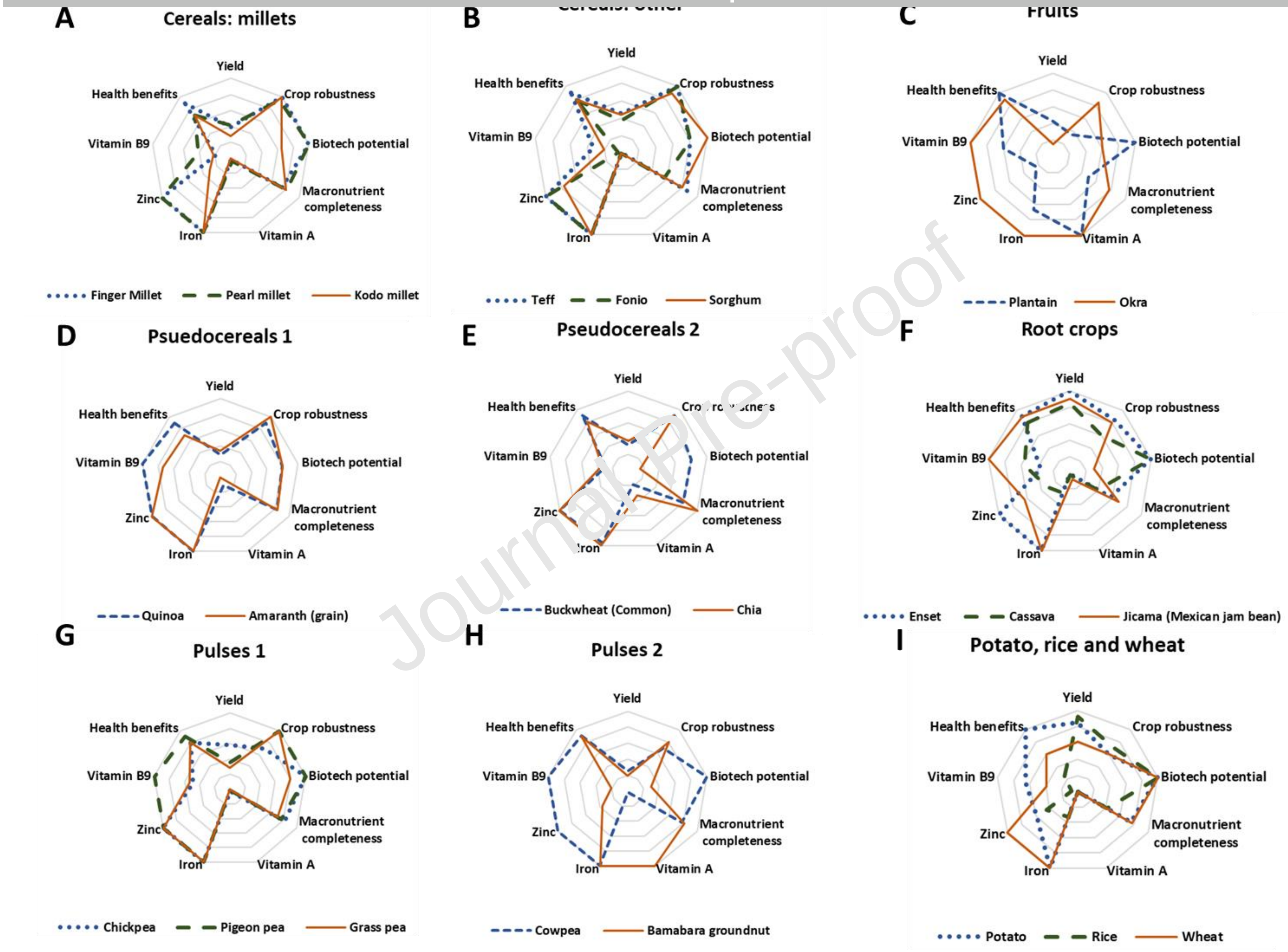
A
Cereals: millets
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Finger Millet
Pearl millet
Kodo millet
B
Cereals: other
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Teff
Fonio
Sorghum
C
Fruits
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Plantain
Okra
D
Psuedocereals 1
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Quinoa
Amaranth (grain)
E
Pseudocereals 2
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Buckwheat (Common)
Chia
F
Root crops
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Enset
Cassava
Jicama (Mexican jam bean)
G
Pulses 1
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Chickpea
Pigeon pea
Grass pea
H
Pulses 2
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Cowpea
Bamabara groundnut
I
Potato, rice and wheat
Yield
Crop robustness
Biotech potential
Macronutrient completeness
Vitamin A
Iron
Zinc
Vitamin B9
Health benefits
Potato
Rice
Wheat

Figure 2: Radar graphs of twenty important orphan crops across the world and three major staples. A: Cereals: millets, finger millet (Eleusine coracana), pearl millet (Cenchrus americanus), kodo millet (Paspalum scrobiculatum); B: Cereals: others, teff (Eragrostis tef), Fonio (Digitaria exilis), sorghum (Sorghum bicolor, Sorghum ssp.); C: Fruits, plantain (Musa × paradisiaca), okra (Abelmoschus esculentus); D: Pseudocereals 1: quinoa (Chenopodium quinoa), amaranth (Amaranthus caudatus L., Amaranthus cruentus L., Amaranthus hypochondriacus L.); E: Pseudocereals 2, buckwheat (Fagopyrum esculentum), chia (Salvia hispanica); F: Root crops, enset (Ensete ventricosum), cassava (Manihot esculenta), jicama (Pachyrhizus erosus); G: Pulses 1, chickpea (Cicer arietinum), pigeon pea (Cajanus cajan), grass pea (Lathyrus sativus); H: pulses 2, cowpea (Vigna unguiculata), Bambara groundnut (Vigna subterranea). I: Major staples, potato (Solanum tuberosum), rice (Oryza sativa), wheat (Triticum aestivum). Crop robustness gives an indication how well the crop copes in high stress environments such as under high temperature and growth on marginal soils. The different parameters on which the crops are scored are yield: average yield + storage robustness; crop robustness: genetic diversity, breeding potential, (a)biotic stress resistance; biotech potential: existence transformation protocol, genome sequenced; completeness: protein, fiber, fat content.; Vitamin A, vitamin B9, iron, zinc: calculation for 50% of recommended daily intake (RDA) in 750 kcal; health benefits: other micronutrient content (Vitamin B1, B6, C and E, Mg, P, Ca), anti-nutritional factors, gluten, anti-oxidant properties, use as medicinal plant.

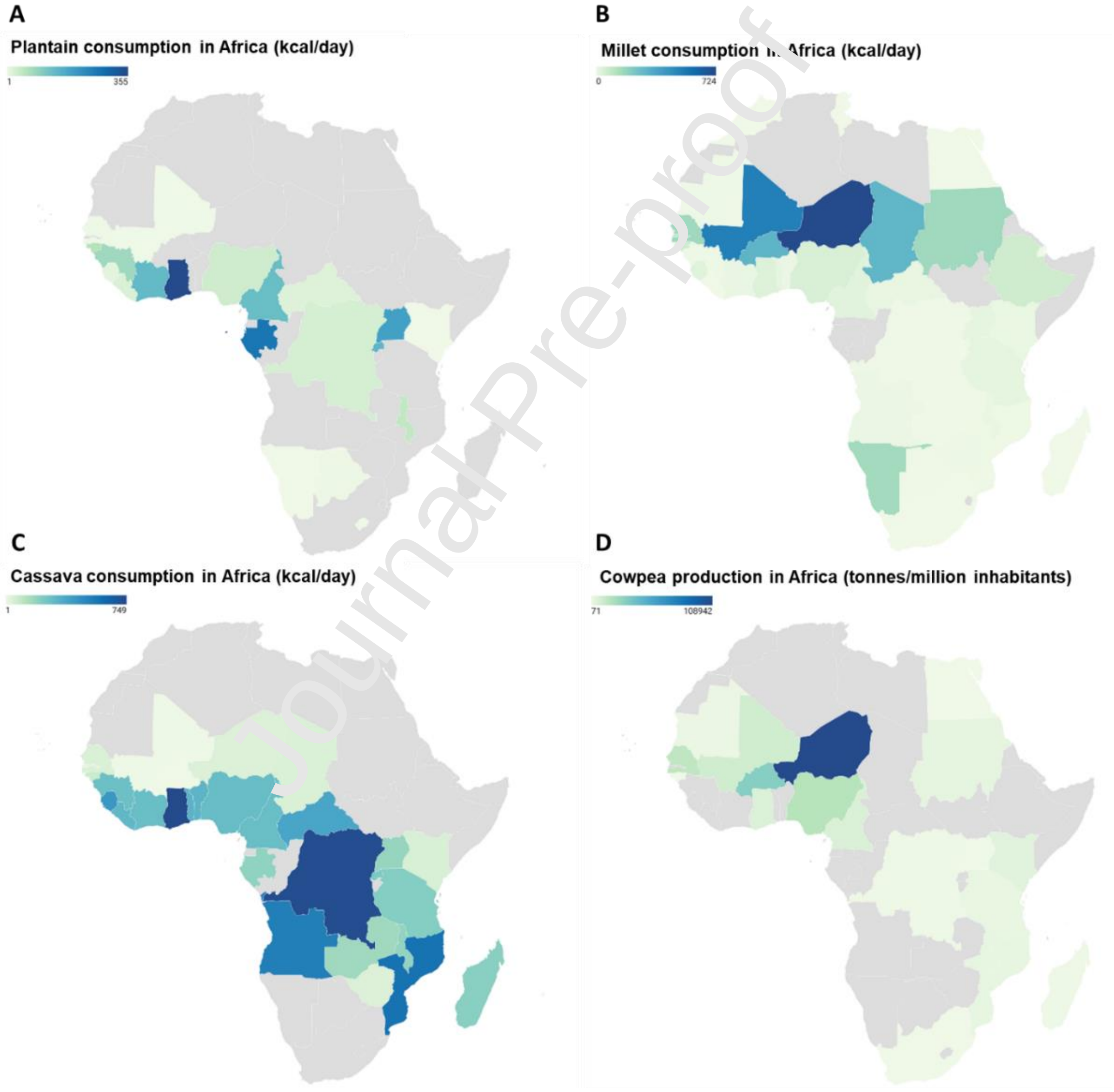

Figure 3: Consumption or production of selected orphan crops in Africa. A, B, C: per capita average daily consumption of plantain (Musa ssp.), millet (Eleusine coracana, Cenchrus americanus) and cassava (Manihot esculenta), respectively in kcal/day. D: for cowpea (Vigna unguiculate) the average production per capita (tonnes/million inhabitants) is shown since no consumption data are available. Source: FAO, 2020. The maps presented here were created with Datawrapper online software.

Biofortification of orphan crops through breeding

Enhancing iron and zinc

Plantain is recalcitrant to conventional breeding since most cultivars are triploid, have low fertility, and high heterozygosity (Jain and Priyadarshan 2009; D'hont 2012). Using genetic engineering (GE) as an alternative route to enhance the iron and zinc content of plantain (Table 2) is therefore of interest, as it would also allow the biofortification of several micronutrients at once (Naqvi 2009; Simrat Pal Singh, Gruissem, and Bhullar 2017). Nonetheless, some reports indicate that certain plantain varieties possess an iron and zinc content ranging from 0,78-2,53 mg iron and 0,22-3,74 mg zinc 100g^{-1} fresh weight (FW) (Honfo, Tenkouano, and Coulibaly 2011; Adepoju 2012). Therefore it is needed to perform a broader screening on iron and zinc content in different plantain cultivars, which could then be used for future breeding programs (H.E. Bouis et al. 2011). Biofortification of cassava for higher mineral content through classical breeding has not been pursued because this root crop lacks adequate biodiversity in minerals such as iron and zinc (Chavez et al. 2000; Narayanan et al. 2019). As such, again, GE has a clear advantage over breeding since it allows introduction of new characteristics into the crop. With respect to millets, high iron content is not consistent in different varieties. In a screening effort of Indian pearl millet varieties, it was shown that iron content ranged from 3,1-10,2mg Fe 100g^{-1} FW (K. Rai 2013). Due to this biodiversity within millets, breeding seems suitable for biofortification, as for instance done by Harvest Plus (H.E. Bouis et al. 2011; K. Rai 2013; Govindaraj et al. 2016). Finally, in cowpea, the iron and zinc content are exceptionally high compared with most of the other orphan crops discussed in this review and relative to the RDA for both micronutrients (Figure 2; Table 2). Notwithstanding, the anti-nutrient content is high as well, reducing bioavailability (Gonçalves 2016). The concentration of phytate in cowpea varies from 0,26–1,5 per 100g; additionally, cowpea also contains high saponin levels (0,25-3,7g per 100g) which further reduces nutrient bioavailability (Gonçalves 2016). There is nonetheless a clear diversity in anti-nutrient levels in different cultivars. Breeding or engineering for lower phytate levels in different varieties would be a relevant attempt in biofortification efforts.

Enhancing folate

To the best of our knowledge, studies reporting diversity of folate levels of plantain have not been published so far. A limited number of studies in banana shows folate content ranging from 13 to 30 µg 100g^{-1} FW (Englberger 2009, Ashokkumar et al. 2018; Ningsih and Megia 2019). Whereas breeding thus seems challenging, GE can step in for folate biofortification of plantain. In contrast, both cassava and millet contain a low amount of vitamin B9 (Table 2). To our knowledge, screening efforts to search cassava or millet cultivars with high folate levels are scant. Recently, limited variation has been reported in the high folate containing foxtail millet (*Setaria italica)* (Sandhya et al. 2020). In the absence thereof, as was the case for iron and zinc, GE becomes the favored method. In cowpea on the other hand, a great variation 177.2 to 780.7 µg 100g^{-1} FW was observed, thereby nicely demonstrating the potential of using high folate germplasm in breeding efforts to increase folate levels of different cowpea genotypes (Nascimento, Cipriano, and Aragão 2022). This is also apparent in other legumes, such as soybean (*Glycine max*) and chickpea (*Cicer arietinum*), where the high folate contents of several cultivars positively point towards the promotion of future breeding efforts (Agyenim-Boateng et al. 2023).

Enhancing provitamin A

Many plantain varieties are rich in pro-vitamin A, yet many highly consumed cultivars contain low amounts of the micronutrient (Kozicka 2021). Consumption of pro-vitamin A rich plantain would nonetheless bring positive health effects in regions struck by VAD (Figure 1; Figure 2;Figure 3) (Amah 2019; Blomme 2020; Kozicka 2021). To address this issue, Harvest Plus is targeting plantain with specific breeding programs to deliver pro-vitamin A rich plantain in sub-Saharan Africa (www.alliancebioversityciat.org/publications-data/promoting-pro-vitamin-rich-bananas-chronology). Both breeding and GE strategies can be followed for this goal. Since extensive literature (Howarth E. Bouis and Saltzman 2017; HarvestPlus, International Center for Tropical Agriculture (CIAT) , Cali, Colombia and Andersson 2017; Amah 2019; CAST 2020) has been produced on the topic of plantain breeding for pro-vitamin A, we will mainly focus on GE here. For cassava, contrary to iron, zinc and folate, several cultivars contain significant amounts of pro-vitamin A (Carvalho 2012; Howarth E. Bouis and Saltzman 2017; Ceballos et al. 2017). Indeed, an elaborate screening effort showed β-carotene content in cassava up to 20,1 ug gFW^{-1} which is equal to 168 µg RAE 100g^{-1} (retinol activity equivalents; 12:1 ratio) (H.E. Bouis et al. 2011). Under a Harvest Plus breeding project (www.harvestplus.org/crop/vitamin-a-cassava/), different yellow root cultivars are grown in Nigeria (Howarth E. Bouis and Saltzman 2017). Pro-vitamin A biofortified cassava was shown to be a good source of vitamin A, lowering vitamin A insufficiency upon consumption (Carvalho 2012; Howarth E. Bouis and Saltzman 2017; Ceballos et al. 2017; Afolami 2021b; 2021a). Breeding is thus a very potent and successful approach to enhance pro-vitamin A levels in cassava. Nonetheless, several transgenic approaches have been followed since breeding cassava is time consuming and difficult (Ceballos et al. 2017), given that genes responsible for high carotenoid content are spread over different loci in the genome which challenges breeders in retaining certain characteristics (including other micronutrients) of local varieties (Ceballos et al. 2017). Additionally, farmers often prefer local varieties. Here, GE clearly has an advantage (Adenle et al. 2012). Finally, for both millets and cowpea, the concentration of pro-vitamin A is very low (Table 2). Thus far, there have been limited efforts for screening carotenoid diversity in different cowpea (Sodedji et al. 2022) or millet cultivars (C. B. Yadav et al. 2021).

*Table 2: The (in)ability of plantain, pearl millet, cassava, and cowpea to supply the recommended daily intake (RDA) for vitamin A, folate, iron, and zinc. The micronutrient concentration of plantain is given in relation to the RDA for non-pregnant women of reproductive age for a reference consumption of 423g or 516kcal plantain per day (Honfo, Tenkouano, and Coulibaly 2011). The micronutrient concentration of pearl millet is given in relation to the RDA for non-pregnant women of reproductive age for a reference consumption of 143g or 516 kcal pearl millet per day. The micronutrient concentration of cassava is given in relation to the RDA for non-pregnant women of reproductive age for a reference consumption of 323g or 516 kcal cassava per day (Moura 2015). The micronutrient concentration of cowpea is given in relation to the RDA for non-pregnant women of reproductive age for a reference consumption of 150g or 516 kcal cowpea per day. Reference RDA (Institute of Medicine (U.S.) and Panel on Micronutrients 2002): iron: 18mg; zinc: 9mg; vitamin B9: 400 µg; vitamin A: 700 µg retinol activity equivalents (RAE). *Note, since molar phytate:iron and phytate:zinc ratios are above bioavailability thresholds (molar ratio > 10) (Honfo, Tenkouano, and Coulibaly 2011), calculations for contribution to RDA for iron and zinc are therefore overestimated (Honfo, Tenkouano, and Coulibaly 2011). **Note, phytate:iron and phytate:zinc ratios are very high in pearl millet, lowering the actual bioavailability of these micronutrients (Krishnan and Meera 2018). FW: fresh weight.*

	Pro-vitamin A (RAE)	Vitamin B9	Iron	Zinc
Plantain *(Musa ssp.)*				
Current % of RDA	34	23	13*	9*
Desired % of RDA	50	50	50	50
Current concentration (µg per 100g FW)	56	22	550	190
Desired concentration (µg per 100g FW)	81	48	2110	1060
Pearl Millet *(Cenchrus americanus or Pennisetum glaucum)*				
Current % of RDA	1	16	64**	49**
Desired % of RDA	50	50	/	/
Current concentration (µg per 100g FW)	5	45	8000	3100
Desired concentration	250	142	/	/

(µg per 100g FW)				
Cassava *(Manihot esculenta)*				
Current % of RDA	0	22	5	12
Desired % of RDA	50	50	50	50
Current concentration (µg per 100g FW)	1	27	270	340
Desired concentration (µg per 100g FW)	109	62	2790	1400
Cowpea *(Vigna unguiculata)*				
Current % of RDA	0	240	83	102
Desired % of RDA	50	/	/	/
Current concentration (µg per 100g FW)	2	64	9950	6110
Desired concentration (µg per 100g FW)	230	/	/	/

Biofortification through genetic engineering

Enhancing iron and zinc

Biofortification of iron and zinc can be accomplished with several strategies. Interesting methods discussed in our analysis include targeting the plantain fruit to enhance iron storage; facilitating iron transport from the iron rich peel (Arun 2015) to the plantain fruit and lowering the high phytate levels to enhance iron bioavailability. The latter methodology is discussed at length since it is transferable between the different crops.

GE-biofortification strategies for improving mineral content typically rely on improving storage capacity of a given target tissue. The common approach is over-expression of the iron binding protein ferritin (Borg 2012; Trijatmiko 2016). Indeed, fruit specific overexpression of soybean (*Glycine max*) ferritin (*GmFER)* in banana cultivar *Rasthali* led to 6.3-fold and 4.6-fold increase in iron and zinc respectively (G. B. S. Kumar, Srinivas, and Ganapathi 2011). Another approach for iron biofortification is by increasing iron translocation in the plant towards the fruits combined with fruit specific *Ferritin* gene expression. In the banana cultivar *Rasthali* the iron content in the leaves and roots reaches up to 15mg and 30 mg $100g^{-1}$ FW respectively (K. Yadav et al. 2017), meaning that a minimal enhancement of translocation could indeed have a desired effect if combined with ferritin expression in the fruits. This can be achieved by altering the endogenous concentration of iron chelating molecules (Trijatmiko 2016). A major class of iron chelating molecules are the phytosiderophores of the mugineic acid (MA) family (

Figure *4*A). Of these, nicotianamine (NA) is an Fe^{2+}-chelator (Higuchi 1999; Inoue 2003). Overexpression of *NA-synthase* (*NAS*) successfully led to enhanced Fe^{2+}-translocation in several crops such as rice and wheat (Trijatmiko 2016; S.P. Singh et al. 2017; Nozoye 2018). Plantain, as nongraminaceous plant, mainly uptakes Fe^{2+} from the soil. Enhancement of nicotianamine concentration by constitutive nicotianamine synthase (*NAS*) overexpression should thus enhance iron translocation in plantain and help in iron biofortification (

Figure *4*A).

An alternative strategy is to redirect iron from the peel to the fruit. A proof of concept of this idea was performed in rice grains, where iron was successfully translocated from the surrounding aleurone tissue to the rice endosperm (Wu, Gruissem, and Bhullar 2019). This was done by expressing Arabidopsis *NATURAL RESISTANCE ASSOCIATED MACROPHAGE PROTEIN* (*AtNRAMP3*) in an aleurone specific manner (Wu, Gruissem, and Bhullar 2019). This transporter exports iron from vacuoles to the cytosol (Wu, Gruissem, and Bhullar 2019). The strategy proved very successful combined with tissue specific ferritin expression. Plantain peel is rich in iron, accumulating up to 6.96 mg iron $100g^{-1}$ FW (Arun 2015), translocation of iron could thus enhance plantain iron content. A challenge lies in identifying peel specific promoters, although this will most likely only require a minimal effort since several elaborate transcriptomic analyses have been performed on banana peels (Mbéguié-A-Mbéguié 2009; Yun 2019).

Mineral bioavailability is highly dependent on anti-nutrient composition in the given crop. The most relevant anti-nutrient is arguably phytic acid or phytate. This compound forms an insoluble complex with iron and zinc at the physiological pH of human intestines, drastically reducing bioavailability of the minerals (Coulibaly, Kouakou, and Chen 2010; Perera, Seneweera, and Hirotsu 2018; Krishnan and Meera 2018). Plantain contains between 0,17-1,23g phytate or phytic acid $100g^{-1}$ dry weight (DW), with phytate:iron and phytate:zinc ratios above bioavailability thresholds, lowering the bioavailability of zinc and iron. Phytic acid content in pearl millet, for instance, ranges from 0,5 – 2g $100g^{-1}$ FW (Coulibaly, Kouakou, and Chen 2010; Krishnan and Meera 2018).

Phytate is needed for proper plant growth as it is the principal storage form of phosphorus in plants. During seed germination, phytases are upregulated and release a usable form of phosphorous from phytate. Targeting phytate in a crop therefore often leads to reduced seed germination (Coulibaly, Kouakou, and Chen 2010; Perera, Seneweera, and Hirotsu 2018). Attempts in other crops to lower phytate have shown a tendency for yield penalties upon complete degradation of phytate (C. S. Reddy, Kim, and Kaul 2017). Several strategies exist, ranging from expressing phytase that breaks down phytic acid to knocking down enzymes in the biosynthetic pathway (Perera, Seneweera, and Hirotsu 2018; Raboy 2020), but no strategy seems to represent a silver bullet. As brought forward by *Raboy (2020)*, perhaps a yield penalty of 5-10% could be acceptable if bioavailability of several micronutrients drastically increases due to lower phytate levels (Raboy 2020). An important remark is that clonally propagated crops, as is the case for plantain, are not necessarily of concern in respect to reduced germination; for these only the effects on yield are of major consideration. Nonetheless, there are reasons to assume that a targeted approach will allow reduction of phytic acid with only a minimal yield penalty and no germination loss.

One such approach consists of lowering phytic acid content in crops by overexpressing phytase in a tissue-specific manner in the seeds (Raboy 2020). A very potent type of phytase for this purpose is the one found in the bacterium *Bacillus subtilis* as it only dephosphorylates until tri-myo-inositol, rather than full degradation as is the case with most plant based phytases (C. S. Reddy, Kim, and Kaul 2017). This causes a small increase of free inorganic phosphate and of lower inositol phosphates that are less potent mineral chelators (Sparvoli and Cominelli 2015). Indeed, engineering of phytases must be performed with the necessary care, as further dephosphorylation would generate an even lower inositol content and more free inorganic phosphate which play a role in many signaling pathways and thus can have a negative impact (C. S. Reddy, Kim, and Kaul 2017). *BsPhytase* expression in a tissue-specific manner should lower phytate levels while limiting a potential yield penalty. Given that public perception favors utilization of plant-based genetic elements, it might be favorable to use a cisgenic approach and identify or engineer several plant-based phytases with a similar function and express them in the target tissue instead.

Similar as to rice and wheat, phytate in millets is mainly localized in the nutrient dense aleurone layer (Jha, Krishnan, and Meera 2015; Krishnan and Meera 2018; Perera, Seneweera, and Hirotsu 2018).

Several studies in rice successfully silenced genes in the phytic acid biosynthetic pathway in an aleurone specific manner (Kuwano et al. 2009; N. Ali 2013; Karmakar 2020). However, the promoter used in the different studies was also active in the embryo (Kuwano et al. 2009), not exclusively in the aleurone layer. One good approach in millet could therefore be to specifically inhibit phytic acid biosynthesis exclusively in the aleurone layer by RNAi-technology. Ideally, to reduce a negative yield or germination impact, the biosynthetic gene responsible for conversion of tri-myo-inositol to phytic acid is targeted rather than silencing the pathway upstream. As such tri-myo-inositol can still serve as a phosphorus source for the germinating seedlings while it has a lower impact on bioavailability (Punjabi et al. 2018; Raboy 2020). It is important to consider that not only phytate poses a problem for mineral bioavailability. For instance, pearl millet (and other millets) contains high amounts of polyphenols which also form complexes with iron and further reduce bioavailability (Krishnan and Meera 2018; Hassan, Sebola, and Mabelebele 2021). GE could be used to mitigate this issue by targeting genes that influence the biosynthesis of polyphenolic compounds in millets; however, this could partly lower the positive health impact of millets (Hassan, Sebola, and Mabelebele 2021).

As for cowpea, most phytic acid in seeds is in the cotyledons (Uzogara, Morton, and Daniel 1990; Gonçalves 2016). In an innovative study a late-biosynthesis gene of the lipid-dependent-pathway (*inositol polyphosphate 6-/3-/5-kinase (GmIPK2)*) was specifically targeted through the expression of a cotyledon-specific RNAi, thereby still allowing biosynthesis of myo-inositol-triphosphate but not phytic acid in the seed (Punjabi et al. 2018). Translating this approach to cowpea could obtain similar successful results with limited side-effects, as this still provides a potent phosphorous source for the emerging seedlings while enhancing micronutrient bioavailability. Since this approach did not result in an observable yield penalty or germination loss in soybean, it is reasonable to expect a similar result in cowpea.

It becomes clear that for all crops, lowering phytic acid content is walking on a tightrope between potential germination loss and yield penalties. Yet, it still holds great potential for the future of iron biofortification. The impact of different processing techniques to prepare food was not considered when accounting for bioavailability. It is important to note that some standard processing techniques such as boiling, soaking and fermentation can have a positive impact on enhancing bioavailability, by for instance breaking down the antinutrients (Devi et al. 2014). Notwithstanding, the actual amount of nutrients available often is negatively impacted when boiling and milling are employed, as they result in breakdown of many vitamins (M. B. Reddy and Love 1999). This is best illustrated by the 10-64% loss in folate content upon boiling leafy vegetables (Maharaj et al. 2015). On the other hand, many orphan crops are rich in enhancers, such as citric acid, which have a positive influence on nutrient bioavailability, examples of this include amaranth and sweet potato (Uusiku et al. 2010).

Enhancing folate

Several studies in crops such as rice (Storozhenko 2007; Blancquaert et al. 2015), potato (*Solanum tuberosum*)(De Lepeleire et al. 2018), tomato (*Solanum lycopersicum*) (Garza, Gregory, and Hanson 2007), lettuce (*Lactuca sativa)* (Nunes, Kalkmann, and Aragão 2009) and others (Simon Strobbe and Van Der Straeten 2017) have shown successful folate enhancement by GE. In rice, folate levels were increased up to 2500µg per 100g FW, making the biofortified cultivar one of the most folate dense crops (Blancquaert et al. 2015). For plantain, the main goal should be folate enhancement rather than enhancing stability, since, in contrast to most other staples, plantain is not stored for long periods, making folate stability less of a concern. Strategies on folate stability are, however, still applicable for millets, cassava, and cowpea, which can be stored for a long period of time.

The final step of folate biosynthesis takes place in mitochondria, while the precursors for biosynthesis, *para*-aminobenzoate (p-ABA) and 6-hydroxymethyldihydropterin (HMDHP), are produced in the plastids and cytosol respectively (

Figure 4B) (Simon Strobbe and Van Der Straeten 2017). One very successful GE strategy consists of overexpressing the genes responsible for biosynthesis of the precursors in the targeted tissue. Indeed, the high folate levels in rice were achieved by overexpressing *aminodeoxychorismate synthase (ADCS)* for p-ABA and *GTP cyclohydrolase I (GTPCHI)* for HMDHP accumulation. This strategy also proved successful in tomato (Garza, Gregory, and Hanson 2007). Based on the current scientific knowledge, we put forward the hypothesis that this strategy should be sufficient to obtain the desired folate levels in plantain (Table 2).

In rice the folate content of kernels was enhanced with more than 150-fold compared to wild-type (Storozhenko 2007; Blancquaert et al. 2015). A similar approach has been applied in wheat and maize, albeit the levels reached were by far not as high as in rice (Liang 2019). It stands to reason that an analogous strategy can be used in millets. Presumably the most efficient approach is by overexpressing Arabidopsis *GTPCHI* and *ADCS* in an endosperm specific manner as was applied in rice rather than using the soybean orthologs as has been done in wheat and maize (Storozhenko 2007; Blancquaert et al. 2015; Liang 2019). Since both pearl, finger and kodo millet already contain between 18-45µg vitamin B9 per 100g FW, a 3-8-fold enhancement is sufficient to achieve the targeted goal (Table 2).

Another interesting strategy is to combine *ADCS* and *GTPCH* overexpression with the expression of the bifunctional enzyme *HMDHP pyrophosphokinase/ dihydropteroate synthase* (*HPPK/DHPS*), which performs the coupling of both precursors in mitochondria, and *folylpolyglutamate synthase (FPGS*), which turns folates into a poly-glutamylated form that is retained within the mitochondria (Blancquaert et al. 2015; De Lepeleire et al. 2018). Successful inclusion of *HPPK/DHPS* and *FPGS* expression was demonstrated in potato tubers (Simon Strobbe and Van Der Straeten 2017; De Lepeleire et al. 2018). This led to a 12-fold enhancement of stable folate content. Since cassava already contains folate to some degree, this strategy is specifically interesting as the necessary fold-enhancement is moderate (Table 2). Lastly, folate stability could be enhanced by introducing a folate binding protein (FBP) in the targeted tissue to shield folates from breakdown (Blancquaert et al. 2015; Simon Strobbe and Van Der Straeten 2017). The major challenge here, however, taking public perception into account, is to find a potent FBP of plant origin (Puthusseri 2018), rather than the FBP of mammalian origin that was used as proof of concept, albeit very successful (Blancquaert et al. 2015).

Enhancing pro-vitamin A

The main objective in pro-vitamin A biofortification is the enhancement of β-carotene in a crop, the most potent form of pro-vitamin A. One of the enzymes targeted in almost all strategies is phytoene synthase (*PSY*), a key regulatory enzyme in carotenoid biosynthesis which is often the rate limiting step (Ye and Beyer 1979; Fraser 2002; Paine 2005; Giuliano 2017).

Germplasm screening in different Indian banana cultivars showed a positive correlation between *Musa acuminata (Ma)PSY1* expression and β-carotene content (Kaur 2017), making *PSY* an interesting target for plantain as well. Indeed, expression of a banana-derived *phytoene synthase (MtPsy2a)* gene led to a significant enhancement in the 'Cavendish' dessert banana, generating a so called 'Golden Banana'(Paul 2017). So far, no reports have been published repeating this strategy in plantain, although overexpressing *PSY* in plantain is promising. The main challenge currently lies in finding promoters that are exclusively active in plantain fruit, and not in any other tissues as was the case for the promoters used for creation of Golden Banana (Paul 2017). This problem needs to be solved for all other biofortification strategies in plantain as well. In addition to *PSY* expression, expression of the *Arabidopsis Orange^{His}* gain of function mutant might be interesting to further enhance β-carotene in plantain as well (L. Li 2012; Yuan 2015; Bai 2016). This gene has a role in chromoplast development and increases the storage stability of β-carotene, next to stabilizing PSY (Osorio 2019). Induction of a single nucleotide polymorphism (SNP) resulting in conversion of a conserved Arginine to Histidine in this *Orange* gene made it a powerful chromoplast inducer (Tzuri 2015; Yuan 2015). Overexpression of the "golden-SNP" containing *AtOrange ^{His}* or wild type (WT) *AtOrange* gene already proved successful in rice, tomato, sweet potato and other plants (Yuan 2015; Bai 2016; Endo et al. 2019; Yazdani 2019; Kim et al. 2021). In conclusion, although breeding towards provitamin A enriched plantains is needed, our assessment highlights that additional enrichment using GE can be promising. On the other hand, combined micronutrient enhancement is a rational way forward (Van Der Straeten 2020).

For cassava, the most successful strategy thus far generated β-carotene content up to 35 µg g^{-1} DW which also showed enhanced shelf life (Beyene 2018). This was achieved through the root-specific expression of two biosynthesis-related genes, *AtDXS* (deoxy-d-xylulose-5-phosphate synthase) from *A. thaliana* and *PacrtB* (phytoene synthase) from the bacterium *Pantoea ananatis*. The high carotenoid content, however, was offset by a drastic reduction in dry matter content and thus a severe yield penalty (Beyene 2018). It was shown that a single nucleotide polymorphism (SNP) in the cassava *PSY2* gene is responsible for β-carotene accumulation in the roots due to increased enzymatic activity (Welsch 2010). Additionally, significant Orange protein accumulation was observed in yellow cassava roots compared to white cassava roots (Jaramillo 2022). Overexpression of cassava *MeOR_X1* together with *ZmPSY* led to very high β-carotene levels in cassava callus (Jaramillo 2022). The cassava *MeOr_X1* gene does not contain the SNP mutation (*Orange^{His}*) referenced previously (Jaramillo 2022). It is thus highly promising to target both the *PSY* and Me*Or_X1* gene of cassava using a gene editing intervention such as CRISPR/Cas to induce the described "golden SNP's" in both genes simultaneously (Welsch 2010; Endo et al. 2019). This should strongly increase carotenoid biosynthesis and create a sink for carotenoids in the root at the same time.

In the case of pulses and legumes, genetic engineering to successfully increase the β-carotene content has been limited to soybean thus far (Schmidt 2015). This knowledge gap poses a challenge to develop strategies for genetic enhancement of β-carotene in pulses. Nonetheless, several reasonable approaches can be thought out based on current knowledge. In soybean, β-carotene levels up to 845µg g^{-1} DW were obtained by overexpression of a bacterial phytoene synthase (*PaCrtB*). However, due to the very strong lectin promoter used in this approach, the protein content of the transgenic beans increased drastically. In chickpea it was found that amongst others, *zeta-carotene desaturase* (*ZDS*) and on a minor level *phytoene synthase (PSY)* were positively correlated with the carotenoid concentration across different cultivars (Rezaei, Deokar, and Tar'an 2016). Projecting these data on legumes in general, it is reasonable to expect that a similar approach as followed in other crops, such as rice and potato, will be successful in legumes like cowpea as well (Paine 2005; Diretto 2007; Giuliano 2017). This approach consists of tissue specific *PSY/CrtB* and *CrtI* expression. Bacterial *CrtI* can perform the four desaturase steps in carotenoid biosynthesis of which *ZDS* is a part. As for all biofortification strategies, the choice of a suitable promoter will be crucial for cowpea as well. Usage of a too strong promoter might bring negative side effects as observed in soybean by increasing the protein content of the seeds drastically, while a too weak promoter might not result in the desired β-carotene accumulation (Ye and Beyer 1979; Schaub 2012).

In cereal crops, pro-vitamin A biofortification has been successfully performed (Giuliano 2017). In maize, β-carotene levels up to 60µg per 100g DW were obtained, while in rice levels up to 37µg β-carotene per 100g DW were obtained (Paine 2005; Naqvi 2009). In both crops the same strategy was used, namely endosperm specific overexpression of *ZmPSY* and *Pantoea ananatis (Pa)CRTI*. Additional to boosting biosynthesis of pro-vitamin A, there is the issue of stability. Beta-carotene, the main plant derived source for vitamin A, is notoriously unstable in certain food matrices as for instance in the rice endosperm (Pénicaud et al. 2011; Bollinedi 2019). It is unclear whether β-carotene would be stable in millets, thus expressing the "golden SNP"-containing *Orange* gene from Arabidopsis in the biofortified tissue to stabilize β-carotene could be a valuable strategy, (Lopez et al. 2008; L. Li 2012; Yuan 2015; Bai 2016; Endo et al. 2019). Overall, it is reasonable to assume that tissue specific expression of *ZmPSY, PaCRTI* and optionally *AtOr*^{His} will lead to pro-vitamin A enhanced millet.

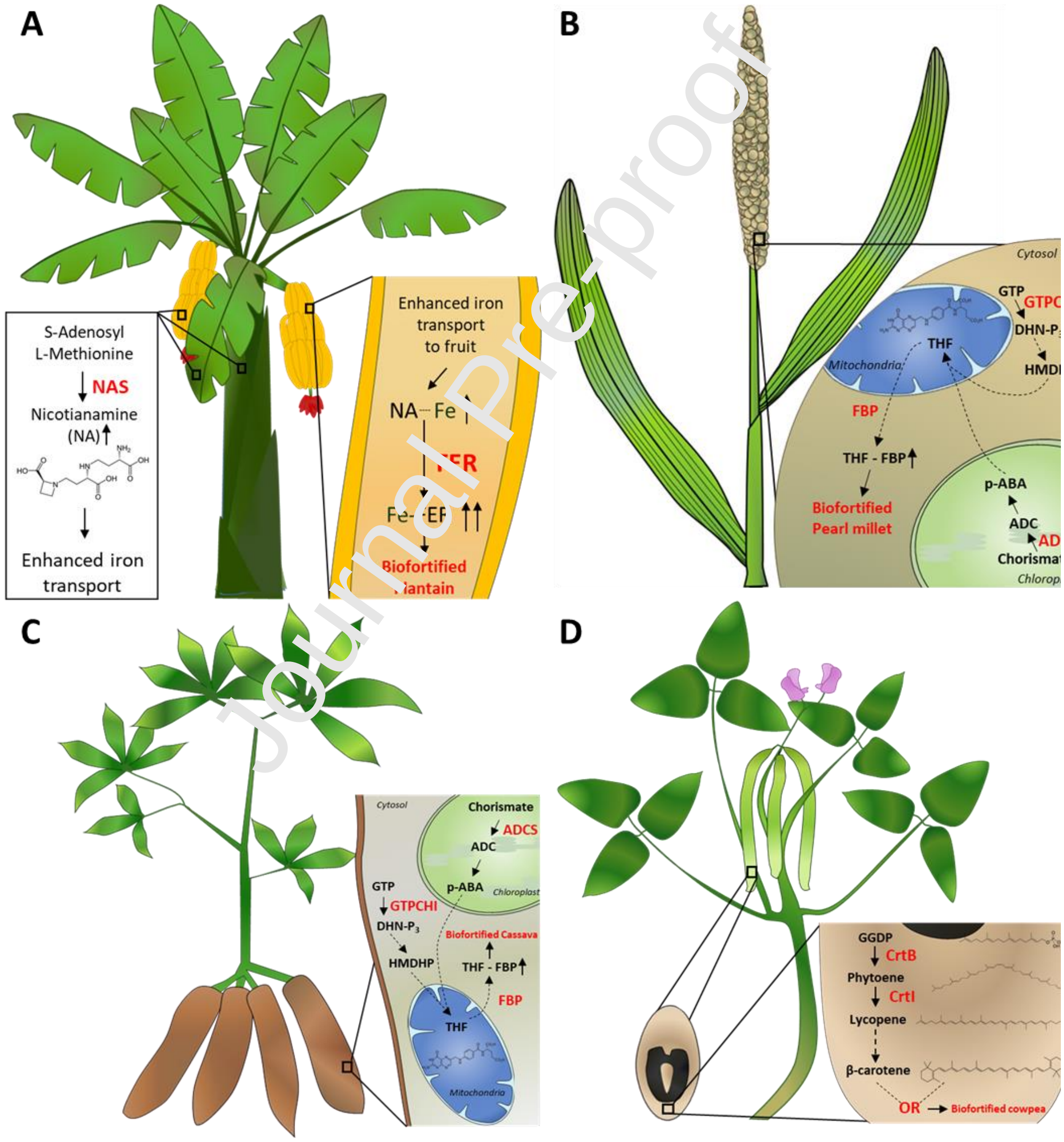

Figure 4: Biofortification strategies for different orphan crops using genetic engineering. A: Development of iron biofortified plantain by constitutive overexpression of *nicotianamine synthase* (*NAS*) and fruit specific expression of *Ferritin* (FER). Nicotianamine (NA) is synthesized by from S-Adenosyl L-methionine by action of NAS. NA enhances iron

transport in the plant through chelation of Fe^{2+}. In the fruit *Ferritin* binds the iron mobilized inwards by NA-Fe chelates creating iron bound ferritin and biofortified plantain. B: Development of folate biofortified millet by endosperm specific overexpression of *GTP cyclohydrolase I (GTPCH), aminodeoxychorismate synthase (ADCS)* and *folate binding protein (FBP)*. In the pterin branch, 6-hydroxymethyldihydropterin (HMDHP) is synthetized from GTP with the first committed step performed by GTPCHI. In the p-ABA branch the first committed step is performed by ADCS, converting chorismate into aminodeoxychorismate (ADC). Both are transported into the mitochondrion by active/passive transport (dotted line) where they are condensed into tetrahydrofolate (THF). THF is transported to the cytosol by active/passive transport and stabilized by FBP, generating folate biofortified pearl millet. C: Development of biofortified cassava by root specific expression of *GTP cyclohydrolase I* (*GTPCH*), *aminodeoxychorismate synthase* (*ADCS*) and *folate binding protein* (*FBP*). See above for description of pathway. D: Development of pro-vitamin A biofortified cowpea by pea specific overexpression of bacterial *Phytoene synthase* (*CrtB*), *Phytoene desaturase* (*CrtI*) and *Arabidopsis Orange (OR)*. CrtB performs the first committed step in carotenoid biosynthesis by condensing two geranylgeranyl diphosphate (GGDP) molecules into phytoene. Phytoene is subsequently converted into all-trans-lycopene by CrtI and converted into β-carotene by endogenous enzymes (dotted arrow). OR induces plastoglobuli and chromoplast formation which stabilizes β-carotene. NAS: Nicotianamine synthase; NA: nicotianamine; Fer: Ferritin; GTP: guanosine triphosphate; GTPCHI: GTP cyclohydrolase I; DHN-P: dihydroneopterin monophosphate; HMDHP: 6-hydroxymethyldihydropterin; THF: tetrahydrofolate; p-ABA: para-aminobenzoate; ADC: aminodeoxychorismate; ADCS: ADC synthase; FBP: folate binding protein; GGDP: geranylgeranyl diphosphate, CrtB: bacterial phytoene synthase; CrtI: bacterial phytoene desaturase; Or: *Orange.* Figure adapted from Strobbe *et al.,* (2017) for folate biosynthesis

Ending hunger in all its forms

Eliminating hunger and malnutrition has been a primary goal of the international community for more than 40 years (*The State of Food Security and Nutrition in the World 2020* 2020). Since around the year 2000, there has been a concerted global effort to present solutions for mitigating hidden hunger (Allen, World Health Organization, and Food and Agriculture Organization of the United Nations 2006). This has resulted in a multi-level approach targeting several fronts. Micronutrient supplementation as well as fortification of food products were deployed on a massive scale, thereby severely reducing the occurrence of deficiencies in the populations addressed (Rautiainen et al. 2016; Imdad et al. 2017; Keats et al. 2019; Tam et al. 2020). Though these interventions have helped relieving hidden hunger for millions of people, their reliance on continuous efforts (e.g., distribution) and specialized infrastructure hampers their sustainability and resilience (Rao 2016). An example of the latter includes the currently witnessed exacerbation of micronutrient malnutrition during the COVID-19 pandemic (Headey 2020; Carducci et al. 2021; Mensi and Udenigwe 2021; Osendarp 2021). On top of the disruption of supplementation programs (Carducci et al. 2021), the COVID-19 pandemic has been reported to have a negative influence on dietary patterns (Fleming and Luo 2021; Rodriguez-leyva and Pierce 2021). This confirms the dire need for additional efforts against micronutrient malnutrition by allowing sustainable, local acquisition of micronutrient-dense food.

Biofortification can provide a sustainable, cost-effective additional strategy in the fight against malnutrition (Howarth E. Bouis and Saltzman 2017; Steur et al. 2017; CAST 2020). These efforts have generally focused on highly consumed staples such as rice (Steur 2015; Tiozon, Fernie, and Sreenivasulu 2021), wheat (M. W. Ali and Borrill 2020; Saini, Devi, and Kaushik 2020; Gupta et al. 2021), maize (Maqbool and Beshir 2019; Goredema-matongera 2021) and potato (Diretto 2007; B. Singh et al. 2021). Yet, for many communities biofortification of their local crops would prove more beneficial since they are often specifically adapted to the environment in which they grow and are part of local diets.

The hypothesized strategies in this review are based on the current scientific knowledge as proven in different species, so their success would need to be experimentally validated. Here, we propose a mode-of-action that demonstrates how biofortification efforts should be deployed. The selected crops are ideal examples for metabolic engineering. Plantain, pearl millet, cassava and cowpea all have a sequenced genome and several transformation protocols have been published for each crop (Figure 1). It is noteworthy to point out that cassava is technically no orphan crop anymore thanks to recent research attention (Amelework et al. 2021). Since cassava is a crop of major importance for sub-

Saharan Africa and research in the crop is still in development, we chose cassava as root crop example, nonetheless. For most other orphan crops this is, unfortunately, not the case. Bambara groundnut for instance has its genome sequenced but is very recalcitrant for genetic transformation, making biofortification through GE very difficult. This immediately shows the biggest weakness of GE, being that applications in less researched crops often are very difficult due to a lack of knowledge about the crop on a molecular level. It is therefore of utmost importance to make use of genetic engineering in combination with conventional breeding to create biofortified crops (Van Der Straeten 2020). Both tools have their inherent limitations, but their combination can have synergistic effects.

Whereas multi-biofortification is very challenging using conventional breeding, it is very feasible through metabolic engineering (Van Der Straeten 2020). The only -but possibly significant- challenge lies in transforming a larger DNA-construct into the crop of interest to target several micronutrients in a single transformation event. Multi-biofortification of specific orphan crops would also boost their value to be implemented in dietary diversification campaigns, advocating for consumption of such nutrient-dense locally produced crops (Amelework et al. 2021).

The role of orphan crops in our agricultural system

The role of orphan crops in the wake of the Covid-19 pandemic

The fight against malnutrition has recently gained an added challenge due to the spread and global impact that COVID-19 has had on human development (Udmale et al. 2020; Osendarp 2021; *The State of Food Security and Nutrition in the World 2021* 2021). Before this pandemic, large areas of the world were already struggling with hunger and poverty; now the pressure has increased and spread to new regions (Udmale et al. 2020). This has proven to be a notable challenge to the resilience of our current food systems, and a reminder that they are not sturdy (Béné 2020). Orphan crops and biofortification can be part of a long-term solution to this systematic fragility. Diversification of our agricultural outputs should be a priority (Hertel et al. 2021), as it minimizes the negative effects of possible future disruptions of staple food production. Thus, the promotion of underutilized, local crops is beneficial. This could aid in reducing our over-reliance on specific crops whilst also contributing to rural economic development (Borelli et al. 2020). Furthermore, because these crops are typically cultivated by marginal populations, it can make them more resilient against possible market fluctuations and improve the substance of their small-scale farmers (Borelli et al. 2020). Improving the nutritional content via biofortification only brings more benefit to orphan crop implementation, as this would help reduce current nutritional gaps of the populations consuming these crops (S. Strobbe and Van Der Straeten 2018). Also, if biofortified orphan crops are widely produced and consumed, diet quality across different regions could improve. As there is a direct link between diet quality and immune function in humans (Childs, Calder, and Miles 2019), this type of intervention would have a positive effect on the health status in targeted regions, and consequently, on productivity and economic performance.

Orphan crops and climate change

Climate change is forcibly driving change within our agricultural system (Kummu et al. 2021). The increasing weather variability witnessed at the moment is expected to worsen in coming decades (Shukla et al. 2019). This will have a significant effect on crop yield (Challinor 2014), and as such calls for adaptation mechanisms that enhance the resilience of our food system. Orphan crops can be key to this problem, as most are adapted to grow in unfavorable conditions (Kamenya et al. 2021). Underutilized plant species have been grown in marginal land, forced to develop stress-coping mechanisms, in order to adapt to the high climate variability that these crops have endured (X. Li, Yadav, and Siddique 2020). This is well illustrated in the high tolerance to drought stress that has been identified in many orphan crops, including finger millet (Krishnamurthy et al. 2016), grass pea (*Lathyrus sativus*) (Campbell 1997), tef (*Eragrostis tef*) (Assefa et al. 2015), Bambara groundnut (Majola, Gerrano, and Shimelis 2021) and quinoa (Hinojosa et al. 2018). Furthermore, orphan crops have also been shown to be able to cope with low-fertility and/or contaminated soil. Examples of this are finger millet (Thilakarathna and Raizada 2015), amaranth (Chinmayee et al. 2012) and African yam bean (*Sphenostylis stenocarpa*) (Nnamani et al. 2021). Hence, it stands to reason that orphan crops can be deployed as part of climate-adaptation agricultural plans.

Concluding remarks

Here, we have examined different separate biofortification strategies for orphan crops. It should be noted that given the typical small-scale consumption of these crops as compared to the major staples as rice, potato, and wheat, such biofortification strategies would be applicable to more confined populations. This would inevitably result in a lower cost-effectiveness of the biofortification interventions. To counteract this issue, multi-biofortification, the simultaneous increase of several micronutrients at once, seems very promising. Indeed, multi-biofortification appears relevant as almost all researched orphan crops have unsatisfactory levels of several micronutrients. The biofortification strategies described here serve as a blueprint in the fight against the most widespread micronutrient deficiencies.

Biofortified orphan crops are the ideal candidates to be included in dietary diversification programs. Their potential applicability in rural regions makes them a more beneficial strategy, as these are often difficult to reach with supplementation programs (Gebremedhin et al. 2014). It is important to assess whether there is an opportunity to enhance micronutrient content by breeding programs as well. Ideally, combination of breeding and genetic engineering (potentially making use of genome editing tools) can be employed to create elite, micronutrient rich (multi-biofortified) staples.

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Competing interests statement

The authors declare no financial or commercial conflict of interest.

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Competing interests statement

The authors declare no financial or commercial conflict of interest.