



Review: Shaping a sustainable food future by rediscovering long-forgotten ancient grains



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ABSTRACT

Genetic erosion of crops has been determined way back in the 1940s and accelerated some twenty years later by the inception of the Green Revolution. Claims that the revolution was a complete triumph remain specious, especially since the massive production boost in the global big three grain crops; wheat, maize, and rice that happened back then is unlikely to recur under current climate irregularities. Presently, one of the leading strategies for sustainable agriculture is by unlocking the genetic potential of underutilized crops. The primary focus has been on a suite of ancient cereals and pseudo-cereals which are riding on the gluten-free trend, including, among others, grain amaranth, buckwheat, quinoa, teff, and millets. Each of these crops has demonstrated tolerance to various stress factors such as drought and heat. Apart from being the centuries-old staple in their native homes, these crops have also been traditionally used as forage for livestock. This review summarizes what lies in the past and present for these underutilized cereals, particularly concerning their potential role and significance in a rapidly changing world, and provides compelling insights into how they could one day be on par with the current big three in feeding a booming population.

1. Introduction

Vavilov's vision a century ago that wild genetic diversity could one day be lost has rung true in the world we live in today. Approximately 90% of the world's calories are provided by less than one percent of the known 250,000 edible plant species [1]. Although the idea has always lingered that the big three grain crops (wheat, *Triticum aestivum*; maize, *Zea mays*; and rice, *Oryza sativa*) are tyrannously weakening global food security, this notion has garnered significant attention in recent years, spurred mainly by the presumption that world grain production per capita will likely decline by at least 14% between 2008 and 2030 [2]. Climate change, which is often associated with an increase in biotic and abiotic stresses leading to crop failure within affected regions, is a major barrier to feeding the nine billion people estimated to inhabit the planet by the mid-century [3,4]. In Africa, for example, maize yields are modeled to decrease by 22–35% by 2030 because of the increasingly variable rainfall patterns and local temperatures [5]. In addition to climate variability, global staple crop production is also threatened by constraints including eroded natural resources, accelerated soil erosion, and land degradation [6]. One critical measure to assure future food security for all is to provide more diversified food sources and agricultural systems [7], which may also bring back the approximately 75% genetic crop diversity that was lost along the way [8]. This loss of

genetic diversity imperils crop advances and undermines sustainable agriculture [9,10].

True cereals and pseudo-cereals, currently furnishing at least two-thirds of the world's food calories, have been a symbol of human life and culture throughout history. In general, both true cereals and pseudo-cereals are grouped together based on their common use as edible starchy grains, rather than their plant biology [11]. Major grain crops were domesticated by ancient civilizations almost four millennia ago, and they are continually being improved and transformed into highly productive crops to feed humankind [12]. On the contrary, hundreds of underutilized crops (also known as minor, neglected, or orphan crops) have either been modestly modified or reverted to the wild until recently [13]. The gluten-free wave, coined in the late 2000s, has breathed new life into a handful of long-forgotten cereal species, such as quinoa (*Chenopodium quinoa*), teff (*Eragrostis tef*), and amaranth (*Amaranthus* spp.) [3,7]. Many notable studies over the last decade have explored these crops' genetic and genomic resources, with the most recent example being the release of quinoa's complete genome sequence [14]. This review highlights the past, present, and the plausible future of these highly potential gluten-free grains as the key representatives of underutilized cereals in shaping a sustainable future.

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2. The brass tacks of trending ancient grains with gluten-free property

2.1. Proso millet

Millet, which belong to the grass family Poaceae (or Gramineae), are small-seeded cereals grown predominantly in the semi-arid tropics of Asia and Africa [15]. Some of the most widely cultivated millet species include proso millet, pearl millet (*Pennisetum glaucum*), finger millet (*Eleusine coracana*), and foxtail millet (*Setaria italica*) [16,17]. In the United States, these cultivated millets are principally used as bird and livestock feed, except for proso millet, which is primarily grown for human consumption [18]. Proso millet, also known as broomcorn and common millet, is a warm-season annual plant native to North China [19,20]. As a C4 crop, proso millet flourishes in arid and semi-arid regions prone to drought and heat, where most major cereals fail to adapt [21]. It requires exceptionally little water to grow and has the shortest growing season (60–90 days) among all true cereals [22]. Dating back to 10,000 BCE, proso millet was cultivated widely across Eurasia and was introduced into North America in the 1880s [23–25]. The exact diploid or tetraploid progenitors of domesticated proso millet are unknown [26], although its relationship to other species in the *Panicum* clade has been explored [19]. The species has been found to show exclusive bivalent formation during meiosis, indicating that it may be an allotetraploid ($2n = 4x = 36$) [17]. The phylogenetic study conducted by Hunt et al. [27] supported the allotetraploid origin of proso millet, suggesting that *P. capillare* ($2n = 2x = 18$) or a close relative was its maternal ancestor. Proso millet's estimated haploid genome size is 1020 Mbp [28]. Among all cultivated millets, only foxtail millet's entire genome of approximately 423 Mbp has been completely sequenced, which occurred in 2012 [29].

2.2. Teff

Teff (alternatively spelled tef) is another warm-season annual from the Poaceae family [30]. Deemed the world's smallest grain, teff is the first sequenced member of the Chloridoideae subfamily, which is comprised entirely of C4 species. The closest cultivated species to teff is finger millet, the only millet that shares this subfamily, with teff's closest subfamily being Panicoideae, which encompasses all other known cultivated millets [31,32]. Teff's diploid progenitors remain unknown [32,33], although some early studies suggest that teff is closely related to the wild allotetraploid, *E. pilosa*, which is characterized by its early maturity and seed shattering [34,35]. Sequence analysis data of the nuclear gene *waxy* and plastid locus *rps16* provide further support for this reported evolutionary relationship [36]. Existing for more than 6000 years, the earliest domesticated teff is thought to have originated from Ethiopia, where it is now grown annually by more than six million farmers [37]. Teff thrives in warm climates and is exceptionally tolerant to drought and heat, making it a reliable staple in its native home for centuries [38]. Its plant residues, particularly its straw, are commonly used as fodder for livestock or building materials for homes [39]. In developed countries such as Australia and the United States, teff has been traditionally grown as a forage crop [40], and its potential as a healthy alternative to wheat remained unexplored until recently [35]. Teff is an allotetraploid species ($2n = 4x = 40$) with a medium-sized genome of approximately 730 Mbp [30,32]. The first teff genome draft was released in 2014, covering 87% of its estimated genome size [32]. This genome draft was recently used to analyze the seed storage protein genes in the subfamily Chloridoideae, and these genes have been shown to evolve rapidly in different grass species, including wheat, maize, and rice [41].

2.3. Quinoa

The centuries-old sacred seed of the Incas, quinoa, which was once

scorned by the Spanish conquistadors, is now known as one of the healthiest grains, which flourishes in hostile environments with poor and salty soil [42]. Lake Titicaca along the border of Bolivia and Peru is considered quinoa's center of origin, and it is predicted to have been domesticated around 7000 years ago [43]. Similar to teff, quinoa is an allotetraploid ($2n = 4x = 36$), originating from two hybridized diploid progenitors [44]. Quinoa is botanically similar to sugar beet (*Beta vulgaris*) and spinach (*Spinacia oleracea*), which are all members of the goosefoot family (Chenopodiaceae), now part of the amaranth family (Amaranthaceae) [45]. Quinoa's genome is approximately 1450 Mbp [46] was recently fully sequenced using single-molecule real-time sequencing [14]. The same study also sequenced two diploid progenitors of quinoa, cañahua or kañiwa (*C. pallidicaule*) and goosefoot (*C. suecicum*), and several of its diploid and tetraploid relatives, including pitseed goosefoot (*C. berlandieri*) and avian goosefoot (*C. hircinum*), casting new light on quinoa's evolutionary history. The study signified that quinoa was likely to have been domesticated independently in both highland and coastal environments, rather than in a single event as predicted previously [14]. In addition, the study reported a total of 2,668,694 SNPs that were specific to quinoa and can be used for various genetic and genomic applications, particularly to analyze the crop's genetic diversity, which remains largely unexplored [14,47]. Quinoa's seed coat naturally contains 2–5% triterpenoid glucosides called saponins, which give the grain an unpalatable, bitter taste [48]. Ward [49] reported that the grain-saponin content in quinoa was a quantitative trait, and the recessive allele at the Sp locus inhibited saponin synthesis in two Bolivian lines. To date, little is known about saponin biosynthesis in quinoa, although several candidate genes underlying its biosynthesis and production have been identified [14,50].

2.4. Amaranth

Amaranth is the collective name for approximately 60 members of *Amaranthus*, another genus in the family Amaranthaceae, which harbors several cultivated species used mainly as grains and leafy vegetables [51,52]. Native to Central and South America, amaranth was presumably first domesticated as a grain crop 8000 years ago by the ancient Aztecs. Like quinoa, amaranth was once a sacred grain of pre-Columbian cultures that faded into obscurity when the Spanish arrived at its native land nearly five centuries ago [53,54]. The grain resurged in the 1970s due largely to its high nutritional value [55]; having exceptionally high levels of lysine, an amino acid that is often lacking in major cereals [56]. Three species of amaranth have been cultivated almost exclusively for grains since ancient times: *A. caudatus* (love-lies-bleeding), *A. cruentus* (red amaranth), and *A. hypochondriacus* (Prince-of-Wales feather) [57]. These species are warm-season C4 annuals that exhibit good drought resistance and can readily adapt to new, extreme environments [58]. Together with two weedy species, *A. hybridus* and *A. quitensis*, they form the hybridus species complex, but the boundaries between these five species are vague [59,60]. A recent phylogenetic analysis conducted by Stetter and Schmid [61] indicates that *A. hybridus* is likely the ancestor of all three cultivated species, while *A. quitensis* may be an intermediate between *A. hybridus* and *A. caudatus*. The number of chromosomes varies among species within the genus *Amaranthus*, which has two established basic numbers of 16 and 17 [62]. The gametic chromosome number, $n = 17$, may originate from $n = 16$ through primary trisomy [63]. Among the five species in the hybridus species complex, only *A. cruentus* has a gametic number of 17 ($2n = 2x = 34$), whereas the other four species, *A. caudatus*, *A. hypochondriacus*, *A. hybridus*, and *A. quitensis*, have gametic numbers of 16 ($2n = 2x = 32$) [63,64]. Nevertheless, all five species possess a genome size near 500 Mbp, indicating that no correlation exists between chromosome number and genome size [61,63].

2.5. Common buckwheat

Another ancient pseudo-cereal with comparable potential to quinoa and amaranth is common buckwheat, a short-season summer annual, which usually completes its life cycle in only around 70 days [65]. Common buckwheat is believed to have originated and been first domesticated in Eastern Asia around 6000 BCE, arriving in Europe around the 1400s, and introduced into North America by the Europeans in the 1600s [66]. The buckwheat genus (*Fagopyrum*) in the Polygonaceae family consists of nineteen known species, with common buckwheat and tartary buckwheat (*F. tataricum* Gaertn.) being the only two cultivated species [67]. Currently, common buckwheat accounts for over 90% of the global buckwheat production, making it the most economically important *Fagopyrum* species worldwide [68]. Nonetheless, tartary buckwheat is considered more important in the Himalayan region, as it can be grown at high altitudes around 3500 m [69]. The first chloroplast genome sequence of tartary buckwheat was recently completed and compared with the genome of common buckwheat's wild ancestor, *F. esculentum* spp. *ancestrale* [70]. Buckwheat generally has more protein than other wheats, maize, and rice [71]. Additionally, its seeds are high in flavonoids, primarily rutin, which has antioxidant and antidyslipidemic effects [71,72]. Rutin concentrations in common buckwheat are lower than other buckwheat species; hence, many studies have attempted to understand the biosynthesis and accumulation of flavonoids in this species [69]. Elucidating the genetic basis of the flavonoid biosynthetic pathway has, however, proved challenging in buckwheat, as well as in other crops such as banana [73,74]. Buckwheat has a diploid ($2n = 2x = 16$) genome of approximately 1200 Mbp [75], which is relatively large compared with other diploid plants, including the model plants *Arabidopsis thaliana*; ca. 135 Mbp [76] and rice; ca. 430 Mbp [77].

3. The why and how of deciphering the potential of underutilized cereals

3.1. Role and significance of underutilized cereals in coping with climate change

Increasing evidence shows that climate change threatens major crop production in many countries, particularly those in the hottest, driest, and most arid regions of the world [3,7,78]. At present, drought is one of the most critical abiotic stresses negatively affecting major cereal productivity [79]. Based on the Palmer Drought Severity Index [80], the percentage of drought-affected areas has risen globally since the 1960s, from approximately 5–10% to 15–25% [78,81]. Many underutilized cereals are relatively more drought-tolerant than most major cereals, one of the more renowned examples being amaranth, which is often hailed as the drought-beater [82–84]. Studies have found that the ability of amaranth to withstand severe drought is closely related to its superior water use efficiency, and the capacity to develop an extensive lateral root system in response to water shortage in soils [85,86]. The water use efficiency in amaranth was found to be higher than some economically important crops, including maize and wheat [58,87]. Teff and proso millet are other C4 plants that are drought-tolerant and can survive in various agro-ecological zones [38,88]. Apart from being regional staples, they have also been traditionally used as forage crops for livestock, especially in the forms of hay and silage [89,90].

Recent reports have also shown that widespread changes in temperature extremes can adversely affect major crop production [79,91]. Maize and wheat yield losses are estimated to nearly double by the 2080s, following increased heat stress at anthesis [91]. A study conducted by Lobell et al. [92] revealed that extreme weather with temperatures above 30 °C has negatively impacted wheat yields in India. Rice yields, on the other hand, have been reported to be negatively affected by higher night temperatures, at 32 °C and above [93]. Some underutilized crops are reported to tolerate temperatures well above

35 °C, including proso millet [94] and teff [95]. Cold stress is another critical factor that threatens the productivity of several major crops, including maize, rice, and soybean, which are sensitive to cold [96,97]. Quinoa is a notable example of underutilized cereal that thrives in cold temperatures as low as –8 °C and survives light frosts [98]. Despite being a C3 plant, quinoa is remarkably drought-resistant, owing to its branched and deep root system [99] and the presence of calcium oxalate in its leaf vesicles, which reduces transpiration [100,101].

Although major cereal productivity in many countries has increased several-fold since the dawn of the Green Revolution [102], these crops are intolerant of nutrient-poor soils and require proper irrigation and high chemical fertilizer and pesticide doses to grow, all of which degrade the soil [103]. A few underutilized cereals have been acclaimed to perform excellently in poor soils, one example being buckwheat [104]. Besides thriving in both infertile and acidic soils, buckwheat has a short growing season of ten weeks or less, making it a good weed suppressor [105]. Quinoa, amaranth, and teff also tolerate poor soils, with the first two also being capable of adapting to saline soils [42]. Salinity stress, along with other previously discussed abiotic stresses, influences the occurrence and spread of pests, pathogens, and weeds [84,106]. Cold stress, for example, impairs gene silencing in plants, weakening their defense mechanisms and making them more susceptible to pathogen infection [104]. Similar to major crops, underutilized cereals are not entirely free of diseases and pests. Nonetheless, they are often more tolerant of some pests and diseases than other crops that grow in their native homes [95,107]. For example, *A. caudatus* and *A. hypochondriacus* were both reported to directly defend against insect herbivores such as aphids [108,109], which are known mainly to infect major grain crops including maize [110] and wheat [111].

The value of underutilized cereals goes far beyond simply being climate-resilient, as many of them are packed with nutritional benefits. Some of these cereals also have an extra boon for being naturally gluten-free [7]. Humans have been consuming gluten-rich grains, such as wheat, for thousands of years, but only recently have the health issues surrounding gluten intake been recognized, most noticeably in developed countries. Gluten, a primary storage protein in dietary wheat is formed by cross-links between gliadin and glutenin molecules [112]. For people with celiac disease, a highly complex immune-related disease with a strong genetic component, briefly ingesting gluten can trigger inflammation and intestinal damage, possibly affecting multiple organ systems [112,113]. Starches from white bread and white rice have been reported to digest readily in the small intestine, leading to a rapid increase in blood glucose, which may be linked to a higher risk of obesity [10]. Public concern is growing that gluten may increase the risk of cardiovascular and metabolic syndromes, and thus, strict gluten avoidance has now become a dietary choice, even among people without celiac disease [10,114,115]. This is especially true in the West where the demand for healthy wheat alternatives and organic products is rising rapidly [3]. This food trend has created a vast demand for gluten-free grains.

The extreme monoculture that has spread throughout agriculture since the inception of the Green Revolution has reduced the genetic differences within varieties [8,116,117]. Decreased crop genetic diversity could lead to significant risks for sustainable food supplies, as genetic resources are essential for both viable and competitive plant breeding [118]. Exploiting underutilized cereal species that are more resilient to certain climates and environments could be vital in expanding agronomic crop productivity in terms of yield and nutrient quality. Apart from buffering crop improvement and food production, genetic diversity also provides regulatory ecosystem services such as controlled soil erosion, reduced greenhouse gas emissions and nutrient cycling [117]. The importance of germplasm collection and underutilized species conservation is currently recognized by various global organizations and institutions, including giants such as the Food and Agriculture Organization of the United Nations (FAO) and Biodiversity International [7].

3.2. A glimpse into the key research areas of underutilized cereals

Recent findings indicate that genetically improving the major grain crops alone will be insufficient to feed the rapidly growing population, mainly because they are unsuited to hostile weather patterns and low-input environments [119]. While many underutilized cereals are more versatile than the major cereals due to their high tolerance to various biotic and abiotic stresses, they have their shortcomings in becoming primary food sources, one of which is their low or erratic yields [7,107,120]. Consequently, this is one priority research area that demands immediate attention and efforts to enhance breeding and genetics in these crops.

Advances in genetic technology, notably next-generation sequencing (NGS), are invaluable for improving major grain crops. Take rice, for example, the completion of its genome over a decade ago has led to the discovery of numerous genes associated with complex traits, such as the *SUB1* gene that confers submergence tolerance [121]. The rice genome has also paved the way for the sequencing of other cereals with larger and more complicated genomes, including maize; ca. 2500 Mbp and wheat; ca. 17,000 Mbp [122]. However, continual improvement of major cereals is essential, more opportunities should be given to underutilized cereals to relish the impressive progress of sequencing technology and other high-throughput genomic approaches, for example, microarrays, which have unraveled many functional genes affecting agronomic traits in major cereals [123]. In fact, several previous studies have shed light on the molecular mechanisms underlying biotic and abiotic stress tolerance for some potential underutilized cereals, including proso millet, teff, quinoa, amaranth, and buckwheat, and several key genes linked to their stress responses have been identified (Table 1). However, progress in the use of marker-assisted selection as part of their breeding program continues to lag overall [123,124].

Socio-economic sustainability is another priority area that requires attention. It should involve technological approaches such as developing eco-innovative strategies for waste prevention and management in urban and suburban areas, as well as non-technological approaches including initiatives to raise awareness, given that underutilized cereals are lesser known outside their regions of origin. Developing countries, such as China and India, are seeing fast-paced population growth as of late, leading to a major shift from rural to urban settings [133,134]. Urbanization is closely associated with economic growth, which often leads to lifestyle and consumption pattern changes, some of which are negative [133]. For example, urban populations tend to consume more expensive nutrient sources, such as organic grains and beans, while consumption of common crops such as major cereals, is lower [133,135]. As such, a balanced development and use of both major and underutilized crops are ultimately what the world needs at present.

Table 1

Examples of recent studies utilizing identified genes linked to biotic and abiotic stress response in promising underutilized cereals and pseudo-cereals.

Species	Gene	Type of tolerance(s)	Reference
<i>Panicum miliaceum</i>	WRKY	Abiotic stresses (incl. drought and heat stresses)	[125]
<i>Eragrostis tef</i>	α -Tubulin	Lodging	[126]
<i>Chenopodium quinoa</i>	AHA	Pathogen resistance	[127]
	BADH	Salt stress	[128]
<i>Amaranthus caudatus</i>	ACA	Aphid resistance	[108]
<i>Amaranthus hypochondriacus</i>	Ah24	Biotic and abiotic stresses (incl. defense against herbivory)	[109]
	NF-YC	Water-deficit stress	[129]
	AhDRG2	Water-deficit and salinity stresses	[130]
<i>Amaranthus cruentus</i>	LEA	Abiotic stresses (incl. oxidant conditions and osmotic stress)	[131]
<i>Fagopyrum esculentum</i>	FeDREB1	Freezing and drought stresses	[132]

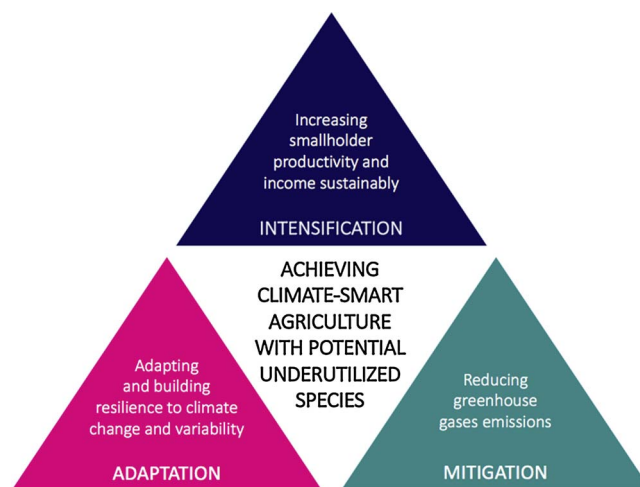


Fig. 1. Towards achieving climate-smart agriculture using underutilized species.

4. Towards achieving sustainable food systems: an agricultural perspective

The past decade has seen radical moves from the scientific community in introducing and developing numerous underutilized crop species, from ancient cereals, such as quinoa and teff, to the “poor man’s pulses” such as chickpea (*Cicer arietinum*) and bambara groundnut (*Vigna subterranean*) [7,84,136,137]. Underutilized species are fast becoming key players in shaping a more diversified global agricultural and food system, which appears to hold great promise for future livelihoods. Not only can the underutilized species be exploited for diversifying food sources and nutritional enrichment, but they can also establish sustainable and resilient agriculture [10,138]. Fig. 1 shows how underutilized species may accelerate the process of achieving climate-smart agriculture through sustainable intensification, adaptation and mitigation. It is worth noting that globalization in the form of the Green Revolution, as much good as has come from it, has somehow created social inequalities over the past decades, almost entirely benefiting the large-scale farmers, while the peasant farmers often live in poverty [7]. Adopting underutilized cereals can, in contrast, help many small-scale farmers, especially those in developing regions that cannot afford high-input agriculture [107]. This may help ensure the farmers’ livelihood, with minimal use of inputs such as land, water, and fertilizer [138,139].

The broader adoption of underutilized crops can also benefit the environment. For example, by growing drought-resistant crops, less irrigation is needed, thus preventing water waste. Similarly, by growing crops that are naturally resistant to certain pests and diseases, certain harmful chemical pesticides can be avoided. All these features make many hardy and versatile underutilized crops the ideal alternative crops for a world undergoing vigorous changes in weather patterns, as well as in food consumption and production patterns [140]. Adopting these crops can also help restore the crop genetic diversity that has been lost over the past century, mainly as a result of monocultures [8,117]. Succinctly, exploiting underutilized crops would directly contribute to several sustainable development goals (SDGs) proposed by the United Nations, including, but not limited to, ending poverty and hunger, assuring healthy lives, and creating resilient and sustainable human settlements (<https://sustainabledevelopment.un.org/sdgs>).

Skepticism surrounding the idea of crop diversification by some researchers, funding agencies and entities is understandable, especially when millions of lives were preserved by merely a few crop types during the Green Revolution. A few fundamental disparities, however, must be recognized and considered if we are to make a valid resemblance of the past to the present. It begs the questions of whether the earth today remains gifted with the same fertile soil as fifty years ago?

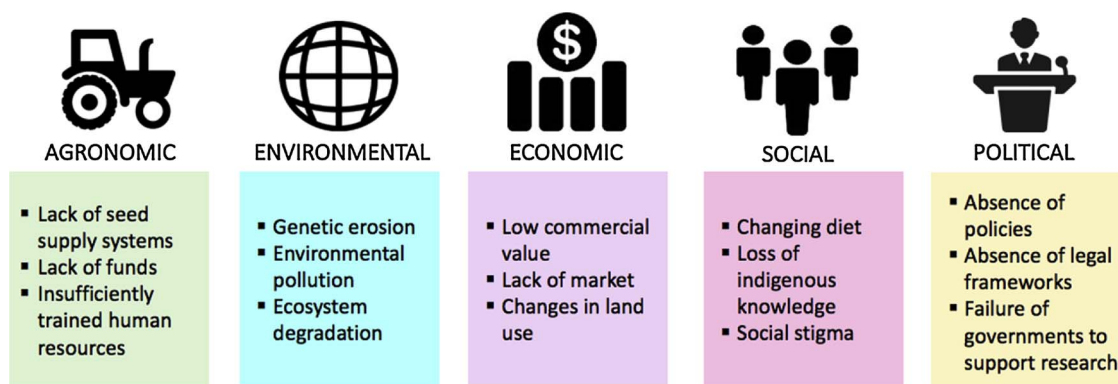


Fig. 2. The major challenges of exploring the potential of underutilized species.

Have the pests of today evolved to become more resistant towards commonly used pesticides? Are changes in the global climate stimulating or deterring major crop yields? We know that the world is different today than it was before, and to a certain extent, we can all agree that the answers to those questions would most likely lean towards the negative. Developing and using underutilized cereals may not save the world overnight, but these cereals' ability to survive the changing planet demonstrates that they are worthy of being explored. Nevertheless, some major challenges lie ahead in fully exploring the potential of these crops [7,141], which are presented in Fig. 2. A concerted global effort from various parties, especially breeders and researchers, is crucial to unleash the full potential of these crops, especially when the possibilities are endless with recent advances in agricultural biotechnology.

5. Conclusion

Many underutilized cereal species are suitable for growing in weather or conditions that are commonly perceived as 'bad', and for this reason, they should be explored, developed, and exploited now more than ever. With their resilience to various biotic and abiotic stresses, underutilized cereals could be the answer to the grim state of food security, while also catering to the nutritional demands of a growing population. These aims are consistent with the current global sustainability agenda on food and nutrition security.

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