

Leveraging millets for developing climate resilient agriculture

McKena Lipham Wilson¹ and Robert VanBuren^{1,2}



C₄ grasses dominate natural and agricultural settings, and the widespread success of wild grasses is mostly attributable to their resilience to environmental extremes. Much of this natural stress tolerance has been lost in major cereals as a byproduct of domestication and intensive selection. Millets are an exception, and they were domesticated in semi-arid regions of Sub-Saharan Africa and Asia where selection favored tolerance and stability over yield. Here, we review the evolutionary and domestication histories of millets and the traits that enable their stress tolerance, broad adaptability, and superior nutritional qualities compared to other cereals. We discuss genome editing and advanced breeding approaches that can be used to develop nutritious, climate resilient cereals of the future. Finally, we propose that millets can play a central role in the global food system to combat food insecurity, with researchers and germplasm from the Global South at the center of these efforts.

Addresses

¹ Department of Horticulture, Michigan State University, East Lansing, MI 48824, USA

² Plant Resilience Institute, Michigan State University, East Lansing, MI 48824, USA

Corresponding author: VanBuren, Robert (bobvanburen@gmail.com)

Current Opinion in Biotechnology 2022, 75:102683

This review comes from a themed issue on **Plant biotechnology**

Edited by **Sonia Negrao** and **Magdalena Maria Julkowska**

For complete overview of the section, please refer to the article collection, "**Plant biotechnology**"

Available online 15th January 2022

<https://doi.org/10.1016/j.copbio.2022.102683>

0958-1669/© 2022 Elsevier Ltd. All rights reserved.

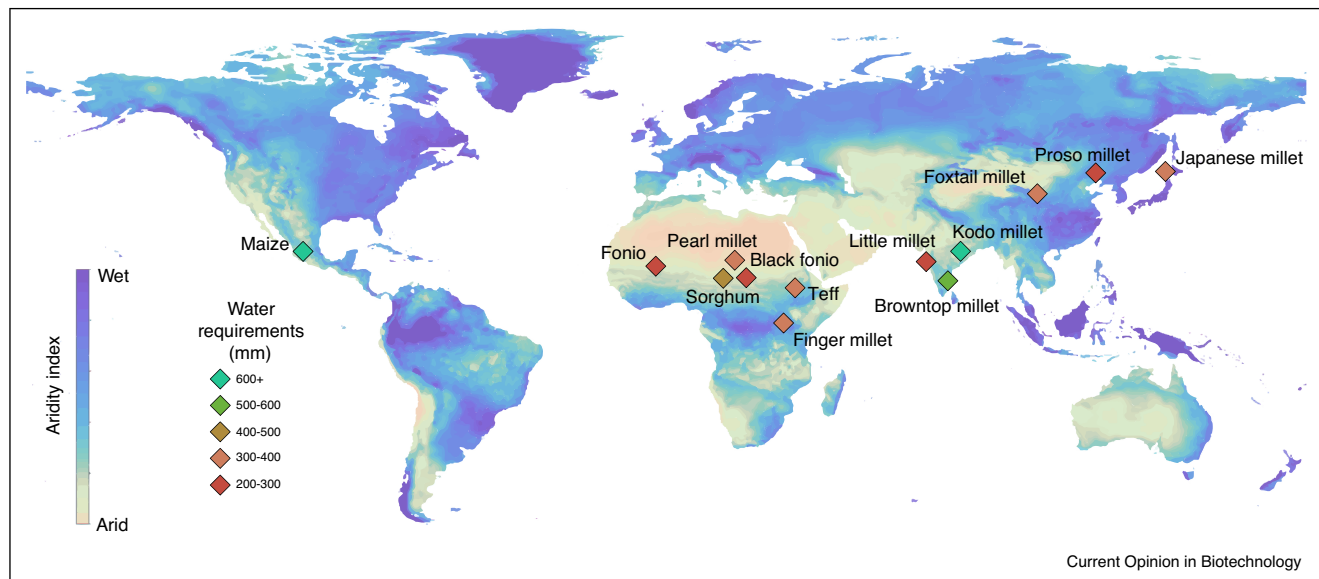
Introduction

The introduction of agriculture nearly 12 000 years ago was built upon the domestication of cereals [1]. Mobile gatherers foraged cereals by hand and through the process of recurrent selection, transformed wild grasses into the staple crops we consume today. This long domestication history provided the necessary time for the development and ultimate globalization of elite cereals [2*]. Grasses dominate the terrestrial landscape and they have evolved a suite of anatomical, physiological, and molecular adaptations that allow them to colonize harsh environments [3]. Humans have domesticated several hundred

phylogenetically diverse grain crops to varying degrees including maize, wheat, rye, sorghum, finger and pearl millet [2*,4]. Cereals are widespread throughout the Poaceae or grass family and originate from two distinct clades: BEP and PACMAD, named for the subfamilies they contain. The BEP clade (Bambusoideae, Ehrhartoideae, and Pooideae subfamilies) includes mostly cool season C₃ cereals such as wheat, barley, rye, and oat, as well as the warm season cereal rice and various bamboos. Grasses in the PACMAD clade (Panicoideae, Arundinoideae, Chloridoideae, Micrairoideae, Aristidoideae, and Danthonioideae subfamilies) utilize C₄ photosynthesis, and generally thrive in regions with high light, warm temperatures, and drier climates. Agronomically important species within PACMAD include sorghum, maize, sugarcane, teff and various millets such as pearl, fonio, foxtail, proso, little and finger millet, among others. Cereals have different evolutionary and domestication histories, and the respective innate and selected traits have shaped their tolerance to abiotic stresses.

Cereals were domesticated in each of Vavilov's historical centers of crop diversity across climates ranging from cold and temperate to hot and sub-arid (Figure 1) [5,6]. Each cereal was shaped by its unique domestication history, traits of their wild progenitors, and the degree and intensity of breeding, improvement, and globalization. Leading cereals such as maize, rice, and wheat were selected for optimized yield under intensive cultivation, and stress tolerance was lost as a byproduct of selection. As a result, leading cereals are susceptible to numerous abiotic stresses, resulting in reductions of grain quality and annual losses exceeding billions of USD [7,8]. Millets are an exception, and although generally lower yielding than leading cereals, they are adapted to dry conditions unsuitable for other grain crops. Millets have a short growing season that can be exploited during warm-seasons and incorporated into existing crop rotations. They require low land investment with minimal inputs of fertilization, water, labor, and management [9]. Millet domestication history is rooted in indigenous practices, and these crops were hand sown, harvested and traded, evolving with the land and with the local people. Millets are often referred to as orphan crops due to their low yield and secondary position to staple crops. However, millets are essential grains providing food security and economic opportunities for farmers and growers throughout Asia and Africa. Although millets are often overlooked by research and agricultural communities in the Global North, they offer nutritious, resilient alternatives to conventional food systems.

Figure 1



Geographic and climatic origins of millets.

The presumed centers of origin for the most globally important millets are highlighted, with the color of each point corresponding to the average water requirements for each species. Aridity index is overlaid on the world map with blue corresponding to the least and yellow/orange to the most arid regions. Data from crop origins were adapted from Ref. [97].

In this review, we discuss the underlying biology and unique domestication history of millets and highlight features that contribute to their stress tolerance and climate resilience compared to other leading cereal crops. We focus on key nutritional qualities, broad adaptability, and genetic potential of millets and how they can be leveraged for trait discovery. We highlight how gene editing and biotechnological approaches can accelerate the domestication process and engineering of elite, high-yielding millets that maintain their climate resilience. Finally, we argue that widespread improvement and cultivation of millets can be a key strategy for developing climate resilient agriculture.

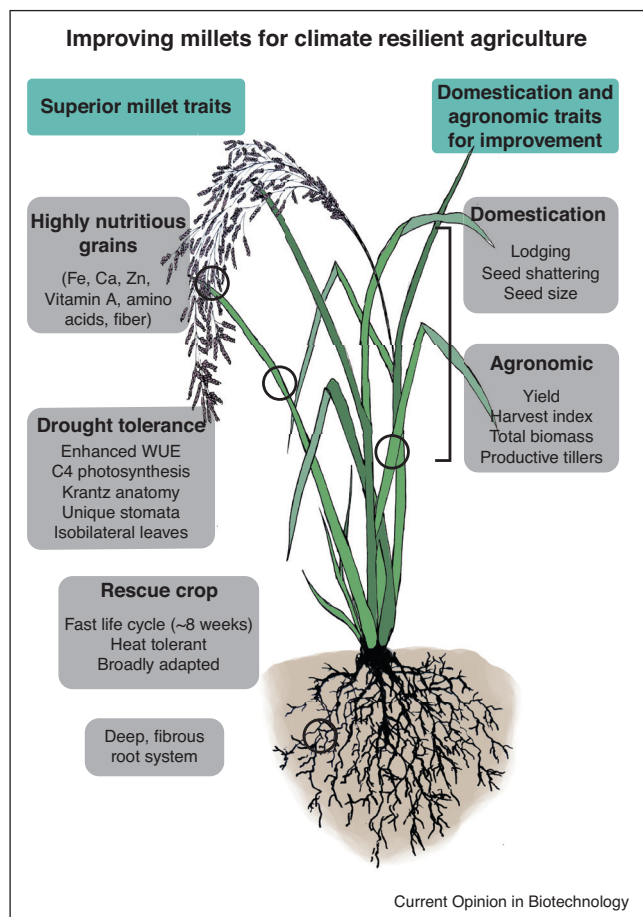
Natural history, resilience, and domestication of millets

Resilience is an emergent property, and stress tolerance requires the coordinated deployment of dozens to hundreds of molecular and phenotypic changes [10]. Some resilience traits are broadly conserved across wild and domesticated grasses and others are specific to millets and their stress tolerant relatives. Many grasses and all millets use the optimized C_4 pathway of photosynthesis, which reduces photorespiration and improves water use efficiency, allowing millets to thrive in warm, dry climates. C_4 grasses have a modified Kranz type leaf anatomy with a ring of mesophyll cells that fix, concentrate, and feed CO_2 in the form of organic acids to inner bundle sheath cells. Decarboxylation of these organic acids creates a CO_2 -rich environment around Rubisco within the bundle sheath

cells to reduce the rate of photorespiration. High vein density and Kranz anatomy of C_4 species also help protect the hydraulic integrity of leaves and maintain a low critical leaf water potential [11,12]. Morphologically, grass leaves have unique dumbbell-shaped guard cells with two subsidiary cells. This modification allows for faster and more refined stomatal responses, resulting in higher water use efficiency [13–15]. Most grasses are amphistomatic, with stomata on both sides of their leaves. These isobilateral leaves held parallel to the axis of irradiance allow for more efficient CO_2 diffusion with low evapotranspiration rates [16]. Paired with their C_4 physiology, deep and fibrous root systems establish quickly to enhance water availability and maintain stability during environmental changes (Figure 2). Overall, a high specific leaf area, net assimilation rate, and root to shoot ratio increase the relative growth rate of C_4 millets [17,18].

The unique resilience of millets can be traced back to their origin and domestication history. The relatively drought susceptible cereal maize was domesticated in the Balsas valley of Mexico which receives ~ 1200 mm of rainfall annually. By contrast, the closely related and drought tolerant millet sorghum was domesticated in the Kassala region of Sudan, which receives only 100–400 mm of rain annually [19]. Fonio, pearl millet, black fonio, African rice, sorghum, teff, and finger millet were domesticated in similarly hot and/or arid regions of sub-Saharan Africa (Figure 1; Table 1). Other millets including kodo millet, foxtail millet, proso millet, and Japanese millet are

Figure 2



Desirable traits and improvement targets for millets. The most desirable traits of millets are highlighted on the left and main domestication and agronomic targets are shown on the right.

endemic to various climatic regions in Southeast Asia with generally low annual rainfall.

Millets have evolved a unique set of adaptations to avoid, survive, tolerate, or recover from water deficit stress [97]. Sorghum, finger millet, and teff have water use efficiencies (WUE) of 4.2–13.4 kg yield -1 ha -1 mm rain; several times higher than comparable C_3 cereals and other grain crops [20]. Cultivated millets have generally low rainfall requirements of 200–500 mm, compared to 500–900 mm for winter wheat and maize, and high WUE helps preserve soil moisture content (Table 1) [21]. Some millets avoid drought altogether like fonio and barnyard millet, which can reach maturity within eight weeks [22]. This short season enables millets to escape unpredictable late summer droughts, or serve as a rescue crop if another grain crop fails. Drought tolerance itself is linked to the evolutionary history of millets, and C_4 grasses express a set of unique, likely ancestral dehydration pathways under severe drought stress that are typically

specific to seed desiccation [23]. When combined with anatomic and physiological adaptations, these dehydration responses allow millets to survive low critical leaf water potential until conditions improve.

Despite their climate resilience, millet production suffers from issues relating to domestication such as seed shattering, low yield, lodging, and poor agronomic practices, and these unfavorable traits have hindered their globalization (Figure 2). Modern millets have a decrease of seed shattering compared to landraces and wild progenitors; however, there are still massive yield losses due to grain shattering, specifically in small millets. Lodging is more prominent in smaller millets as well and has led to reduced grain weight, grain yield per panicle, and seed germination, with a yield loss averaging 25% [24–26].

Superior agronomic and nutritional traits of millets

Millets are culturally and economically important to cities, tribes, and communities across Asia and Africa [27–29]. It is essential we acknowledge the history of these species, their cultural importance, and the traditional practices that have shaped their cultivation. Millets offer an exciting opportunity to enhance agrobiodiversity and amplify other underutilized crops around the world. The diversity in agronomically important crops is continually decreasing, with approximately 60% of global crop output in 2019 coming from rice, wheat, soy, and maize alone [30]. Yet, there are around 6000 plant species cultivated for food, and this diminishing agricultural diversity is a threat to food security, human health, and environmental stability. The introduction of ancient crops originating from seasonally dry climates can counteract agricultural homogenization and may be beneficial in times of climate variability [2^{*}]. Drought is the most pervasive issue in agriculture and the effects of drought are most severe in developing regions such as Sub-Saharan Africa, where ~43% of land is already classified as arid [31]. Millets were domesticated and subsequently selected to tolerate extreme and erratic environments, and cultivation of these cereals can improve productivity of arid landscapes and establish food security under a changing climate.

Leading cereals have inherently low micronutrient concentrations, and overreliance on these crops leads to micronutrient deficiencies, which are observed in 1 of 9 humans [32^{*},33]. Millets have broader micronutrient profiles that can meet the cereal demand and provide sustainable nutritional security (Figure 3). For example, teff flour is exceptionally rich in iron (>50 mg/100 g) and some teff cultivars contain eightfold more iron than the leading cereals maize and wheat [34,35]. Teff seed is high in soluble dietary fiber, has a balanced amino acid content, and contains high levels of Vitamins A and C [36]. Finger millet is extremely calcium rich and has a higher

Table 1

Comparison of resilience and agronomic of leading C₄ cereals and millets

Crop	Scientific name	Grass subfamily	Climate	Stress tolerance	Water requirement (mm)	Growing season length	Minimum yield range (T × H ⁻¹)	Maximum yield range (T × H ⁻¹)
Maize	<i>Zea mays</i>	Panicoideae	Tropical/temperate		500–750	4–5 months	1	20
Sorghum	<i>Sorghum bicolor</i>	Panicoideae	Tropical/temperate	Drought, waterlogging, and salt tolerance	450–650	3–4 months	2	6
Teff	<i>Eragrostis tef</i>	Chloridoideae	Tropical/temperate	Water logging and drought tolerance	300	2–5 months	0.2	4.5
Finger millet	<i>Eleusine coracana</i>	Chloridoideae	Temperate	Drought and salt tolerance	350	3–6 months	0.25	5
Proso millet	<i>Panicum miliaceum</i>	Panicoideae	Arid tropical	Drought tolerance	200–300	2–3 months	0.45	2
Pearl millet	<i>Cenchrus americanus</i>	Panicoideae	Arid tropical	Drought and heat tolerance	350	2–3 months	0.25	8
Fonio	<i>Digitaria exilis</i>	Panicoideae	Tropical/temperate	Drought tolerance	250–350	2–3 months	0.6	1
Foxtail millet	<i>Setaria italica</i>	Panicoideae	Tropical/temperate	Drought tolerance	300	2–4 months	0.8	11
Japanese barnyard millet	<i>Echinochloa crusgalli</i>	Panicoideae	Tropical/temperate	Drought tolerance	310	2–3 months*	1*	3*
Kodo millet	<i>Paspalum scrobiculatum</i>	Panicoideae	Tropical/temperate	Drought tolerance	800	4–6 months	2.8*	4.5*
Little millet	<i>Panicum sumatrense</i>	Panicoideae	Tropical/temperate	Drought and salt tolerance	150	2–5 months	0.225	0.9
Browntop millet	<i>Brachiaria ramosa</i>	Panicoideae	Tropical/temperate	Drought and heat tolerance	440	2–3 months*	1.8	4

Various agronomic traits, climate, and stress tolerance are reported for the leading cereal maize and the most important millets. Data was collected from the Useful Tropical Plants Database [76] with several exceptions. Barnyard millet growing season length and yield range were sourced from Refs. [39] and [77], respectively. Browntop millet growing season length was sourced from Ref. [78] and Kodo millet yield range from Ref. [79].

* Denotes instances where data was missing from the Useful Tropical Plants Database and was collected from the referenced sources.

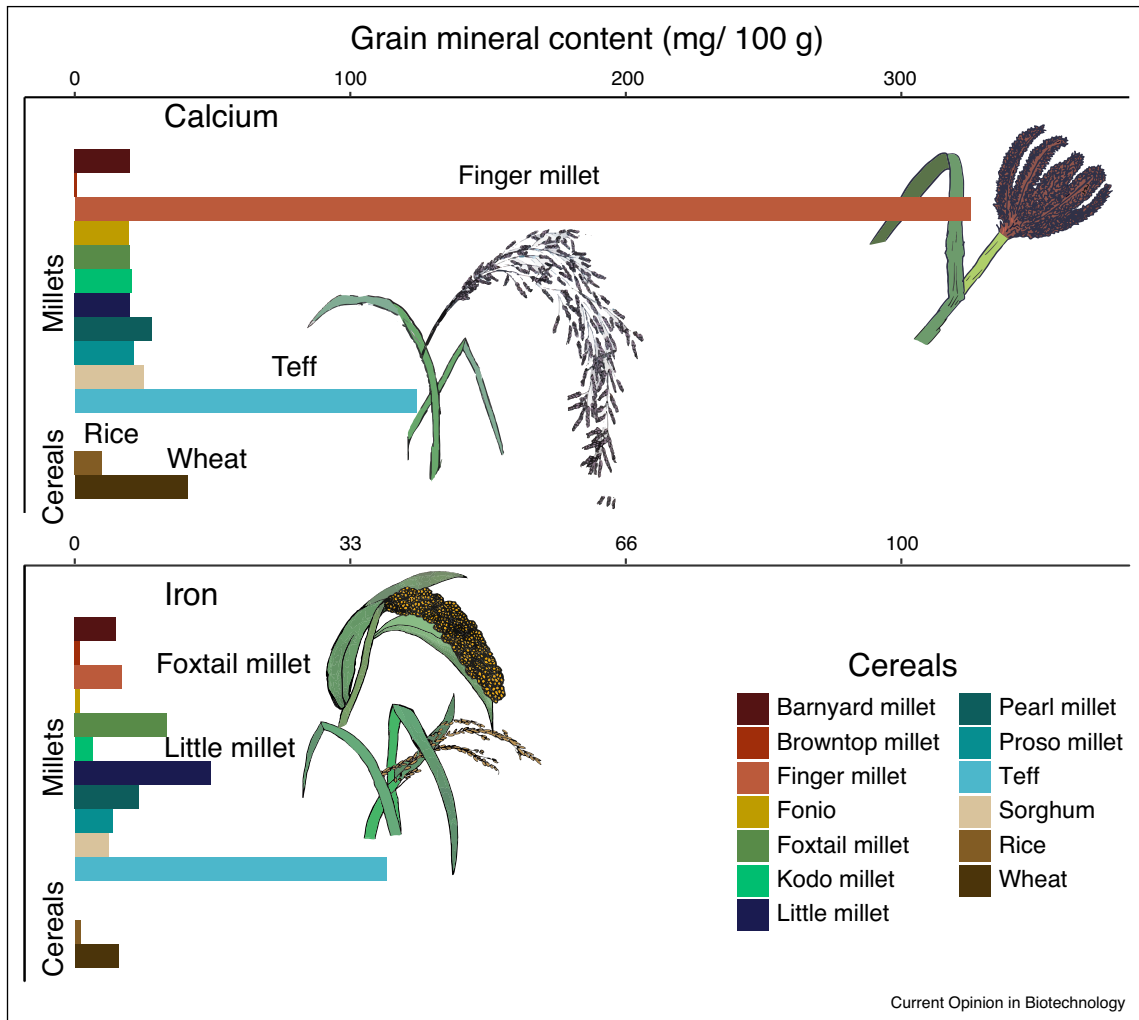
fiber and mineral content than those of rice and wheat (Figure 3) [37]. Like many millets, it is relatively high in protein, with a balanced amino acid profile abundant in lysine, threonine, and valine commonly lacking in other cereals with high starch content [38]. Barnyard millet is the most fibrous of cereals with 8.1–16.3% crude fiber content, and regular consumption of barnyard millet is linked to improved blood glucose maintenance and a lower glycemic index [39,40]. Furthermore, millets may serve as alternatives to wheat flour for those with celiac disease. The environmental resilience and nutritional quality of millets make them ideal model systems to study the effects of stress on resource allocation and crop nutrient production.

Designing millets for resilient agriculture in the 21 century

A shift in focus from staple cereals to highly resilient millets is crucial for the future of the agricultural industry. By promoting the cultivation of alternative grains, we see the potential for heightened agrobiodiversity in our diets, a decrease in micronutrient deficiencies, and reduction of agricultural water, fertilizer, and pesticide demand [41*]. Despite their agricultural potential, millets have lower yield than conventional cereals and production suffers

from incomplete selection of several critical domestication traits such as lodging, seed shattering, and seed size. Limited funding and insufficient phenotypic, quantitative genetic, and agronomic data have hindered the agricultural development of millets in their native regions across the Global South and worldwide. However, recent advances in large-scale biology have made genomic, phenomic, computational, gene editing, and advanced breeding applications more accessible. Genomes for foxtail millet, pearl millet, proso millet, finger millet, fonio, sorghum, and teff have been sequenced [42*,43–48]. Diversity panels of wild, landrace, and elite germplasm have been curated for most millets and detailed population genetics and domestication studies have been performed for sorghum, proso, fonio, finger, and pearl millet [49–51,42*,52]. Genome wide association studies have made use of these genomic resources for mapping agronomic and nutritional traits in finger millet, pearl millet, teff, and proso, but these studies were mostly based on low resolution markers with limited trait information [53–56]. Phenotyping has become the rate limiting step for most millet breeding programs, and outside of foxtail, millets have lagged behind other cereals in the development and implementation of high-throughput phenotyping approaches to quantify complex agronomic traits [57].

Figure 3



Key seed nutritional traits in millets compared to conventional cereals. Seed calcium and iron content is shown for a variety of millets and two leading, conventional cereals (rice and wheat). Values were taken from Refs. [72–75,35], and are reported as milligrams of mineral content per 100 g of dry seeds.

These recent advancements in millet are promising, but lack foundational knowledge of the underlying genetic mechanisms that make millets so resilient, and any trade offs that may exist between stress tolerance and yield. Resilience is complex, and it is unlikely tolerance traits can be distilled into discrete genetic elements for translation into conventional grain crops. Instead, efforts should be focused on integrating millets into our global food system and leveraging advanced biotechnological and breeding approaches to accelerate the development of elite lines that are competitive with conventional cereals. CRISPR–Cas9 mediated breeding approaches have been used to accelerate domestication of African rice landraces through engineering reduced lodging and increased yield and to *de novo* domesticate wild tomato using six loci for yield and productivity [58*,59,60].

Efficient tissue culture and regeneration are often the limiting factors of successful transformation, and species specific optimizations such as explant tissue and growth stage, *Agrobacterium* strain, and infiltration method are necessary for successful gene editing in millets [61–65]. The overexpression of maize morphogenic regulators *Baby Boom* and *Wuschel2* have improved transformation frequencies in sorghum, sugarcane, and rice and these advances can be adapted to recalcitrant millets [66,67]. Dozens of domestication genes have been characterized in leading cereals related to lodging tolerance, seed shattering, grain size, yield, and plant architecture, and new alleles could be engineered to rapidly improve agronomic traits in millets (Table 2). Several multinational initiatives such as the future crops design project are planning to use genome engineering and advanced

Table 2

Gene targets for improved domestication of millets

Trait	Gene	Function	Cereal	Reference
Shattering	Sh1	Transcription factor	Sorghum	[80]
	qSH1	Transcription factor	Rice	[81]
	sh4	Transcription factor	Rice	[82]
Grain filling and size	GIF1	Cell-wall invertase	Rice	[83]
	Gn1a	Cytokinin oxidase	Rice	[84,85]
	GW2	RING-type protein	Rice	[86,87]
	GW5	Calmodulin binding protein	Rice	[88]
	GS5	Serine carboxypeptidase	Rice	[89]
Plant architecture	tb1	Transcription factor	Maize	[90]
	dw3	Auxin transporter	Sorghum	[91]
	PROG1	Transcription factor	Rice	[92]
	IPA1	Transcription factor	Rice	[93,85]
	Dep1	Phosphatidylethanolamine-binding protein	Rice	[94,85]
	SD1	Gibberellin biosynthetic enzyme	Rice	[95]
	Moc1	GRAS family nuclear protein	Rice	[96]

breeding approaches to *de novo* domesticate wild species, and re-domesticate underutilized crops [68*]. These initiatives can provide a framework for quickly improving domestication and yield-related traits in millets and other underutilized crops, but fundamental understanding of millet resilience is still needed to identify target traits.

The improvement and globalization of millets must lead with information obtained from local and indigenous communities at the forefront of millet production, and elite cultivars should include traits that reflect local farming practices and preferences (Figure 2). The breeding targets of local communities can be at odds with global markets as is the case with teff, where Ethiopians prefer white teff flour to make injera bread, but Western communities prefer red or brown teff varieties for their superior nutritional profiles [69]. Millets are mostly grown by small-scale subsistence farmers across the Global South, and thousands of locally adapted cultivars with tremendous diversity and superior environmental adaptability have been developed [70]. This local germplasm can serve as the central foundation for applying gene editing and advanced breeding approaches to develop resilient, high yielding millets, with efforts led by countries with historical ties to millet production. Efforts aimed at building research capacity for the stewards of these crops and decolonizing science will mobilize millet development and maintenance of a rich genetic diversity.

Conclusions

The global production of millets has declined over the past two decades because of growing demand for major cereals like rice, wheat, and maize [71]. Despite this shift, millets have unparalleled adaptability and climate resilience among grain crops, and they can play a central role in improving food security and maintaining cultural traditions. Their generally low yield and related agronomic

issues have branded millets as ‘orphan cereals’, but this is a matter of perspective. Resilience traits in millet stem from their unique evolutionary history, domestication in semi-arid regions, and continual selection for stability over yield. The broad resilience of millets will be difficult to replicate in conventional cereals because of the complex genetic basis of abiotic stress tolerance, and instead, efforts should focus on improving yield traits in millets and shifting the global production toward these important underutilized crops.

Funding

This work was supported in part by funding from the National Science Foundation (NSF-MCB 1817347 to R. V.) and a training fellowship to M.L.W. from the National Science Foundation Research Traineeship Program (NRT 1828149) at Michigan State University.

Conflict of interest statement

Nothing declared

Data availability

No data was used for the research described in the article.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
1. Purugganan MD: **Evolutionary insights into the nature of plant domestication.** *Curr Biol* 2019, **29**:R705-R714.
 2. Milla R, Osborne CP: **Crop origins explain variation in global agricultural relevance.** *Nat Plants* 2021, **7**:598-607
- A meta-analysis on the origin and cultivation of 866 crops found that grain crops originating from seasonally dry environments are cultivated more widely, and older crops tend to have more global importance.
3. Linder HP, Lehmann CER, Archibald S, Osborne CP, Richardson DM: **Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat**

- transformation.** *Biol Rev* 2018, **93**:1125-1144 <http://dx.doi.org/10.1111/brv.12388>.
4. Meyer RS, DuVal AE, Jensen HR: **Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops.** *New Phytol* 2012, **196**:29-48.
 5. Purugganan MD, Fuller DQ: **The nature of selection during plant domestication.** *Nature* 2009, **457**:843-848.
 6. Harlan JR: **Agricultural origins: centers and noncenters.** *Science* 1971, **174**:468-474.
 7. Mantri N, Patade V, Penna S, Ford R, Pang E: **Abiotic stress responses in plants: present and future.** *Abiotic Stress Responses in Plants*. 2012:1-19 http://dx.doi.org/10.1007/978-1-4614-0634-1_1.
 8. Rippey BR: **The US drought of 2012.** *Weather Clim Extremes* 2015, **10**:57-64.
 9. Miller NF, Spengler RN, Frachetti M: **Millet cultivation across Eurasia: origins, spread, and the influence of seasonal climate.** *Holocene* 2016, **26**:1566-1575.
 10. Bray EA: **Plant responses to water deficit.** *Trends Plant Sci* 1997, **2**:48-54.
 11. Sage RF: **Environmental and evolutionary preconditions for the origin and diversification of the C₄ Photosynthetic Syndrome.** *Plant Biol* 2001, **3**:202-213.
 12. Taylor SH, Hulme SP, Rees M, Ripley BS, Woodward FI, Osborne CP: **Ecophysiological traits in C₃ and C₄ grasses: a phylogenetically controlled screening experiment.** *New Phytol* 2010, **185**:780-791.
 13. Lawson T, Violet-Chabrand S: **Speedy stomata, photosynthesis and plant water use efficiency.** *New Phytol* 2019, **221**:93-98.
 14. McAusland L, Violet-Chabrand S, Davey P, Baker NR, Brendel O, Lawson T: **Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency.** *New Phytol* 2016, **211**:1209-1220.
 15. Stebbins GL, Shah SS: **Developmental studies of cell differentiation in the epidermis of monocotyledons. II. Cytological features of stomatal development in the Gramineae.** *Dev Biol* 1960, **2**:477-500.
 16. Drake PL, de Boer HJ, Schymanski SJ, Veneklaas EJ: **Two sides to every leaf: water and CO₂ transport in hypostomatous and amphistomatous leaves.** *New Phytol* 2019, **222**:1179-1187.
 17. Atkinson RRL, Mockford EJ, Bennett C, Christin P-A, Spriggs EL, Freckleton RP *et al.*: **C₄ photosynthesis boosts growth by altering physiology, allocation and size.** *Nat Plants* 2016, **2**:16038.
 18. Simpson KJ, Bennett C, Atkinson RRL, Mockford EJ, McKenzie S, Freckleton RP *et al.*: **C₄ photosynthesis and the economic spectra of leaf and root traits independently influence growth rates in grasses.** *J Ecol* 2020, **108**:1899-1909.
 19. Fuller DQ, Stevens CJ: **Sorghum domestication and diversification: a current archaeobotanical perspective.** In *Plants and People in the African Past: Progress in African Archaeobotany*. Edited by Mercuri AM, D'Andrea AC, Fornaciari R, Höhn A. Cham: Springer International Publishing; 2018:427-452.
 20. Hadebe ST, Modi AT, Mabhaudhi T: **Drought tolerance and water use of cereal crops: a focus on sorghum as a food security crop in sub-Saharan Africa.** *J Agron Crop Sci* 2017, **203**:177-191.
 21. An P, Ren W, Liu X, Song M, Li X: **Adjustment and optimization of the cropping systems under water constraint.** *Sustain Sci Pract Policy* 2016, **8**:1207.
 22. Kumar A, Tomer V, Kaur A, Kumar V, Gupta K: **Millets: a solution to agrarian and nutritional challenges.** *Agric Food Secur* 2018, **7**:1-15.
 23. Pardo J, Man Wai C, Chay H, Madden CF, Hillhorst HWM, Farrant JM *et al.*: **Intertwined signatures of desiccation and drought tolerance in grasses.** *Proc Natl Acad Sci U S A* 2020, **117**:10079-10088.
 24. Chanyalew S, Ferede S, Damte T, Fikre T, Genet Y, Kebede W *et al.*: **Significance and prospects of an orphan crop tef.** *Planta* 2019, **250**:753-767 <http://dx.doi.org/10.1007/s00425-019-03209-z>.
 25. Tian B, Luan S, Zhang L, Liu Y, Zhang L, Li H: **Penalties in yield and yield associated traits caused by stem lodging at different developmental stages in summer and spring foxtail millet cultivars.** *Field Crops Res* 2018, **217**:104-112.
 26. Bayable M, Tsunekawa A, Haregeweyn N, Ishii T, Alemayehu G, Tsubo M *et al.*: **Biomechanical properties and agro-morphological traits for improved lodging resistance in Ethiopian tef (*Eragrostis tef* (Zucc.) Trotter) accessions.** *Agronomy* 2020, **10**:1012.
 27. Adoukonou-Sagbadja H, Dansi A, Vodouhè R, Akpagana K: **Indigenous knowledge and traditional conservation of fonio millet (*Digitaria exilis*, *Digitaria iburuua*) in togo.** *Biodivers Conserv* 2006, **15**:2379-2395.
 28. Li Y, Wu S: **Traditional maintenance and multiplication of foxtail millet (*Setaria italica* (L.) P. Beauv.) landraces in China.** *Euphytica* 1996, **87**:33-38.
 29. Khattri MB: **Climate change, millet and ritual relationship with the Magars of Argal, Baglung, Nepal.** *Dhaulagiri J Sociol Anthropol* 2012, **6**:107-124.
 30. FAO: *Faostat: FAO Statistical Databases*. Rome, Italy: Food & Agriculture Organization of the United Nations (FAO); 2000.
 31. Woldeyohannes AB, Accotto C, Desta EA, Kidane YG, Fadda C, Pè ME *et al.*: **Current and projected eco-geographic adaptation and phenotypic diversity of Ethiopian tef (*Eragrostis tef*) across its cultivation range.** *Agric Ecosyst Environ* 2020, **300**:107020.
 32. Gashu D, Nalivata PC, Amede T, Ander EL, Bailey EH, Botoman L *et al.*: **The nutritional quality of cereals varies geospatially in Ethiopia and Malawi.** *Nature* 2021, **594**:71-76
- Soil and environmental covariates were shown to play a massive role in seed quality and mineral nutrition across grain crops from Malawi and Ethiopia, and this should be accounted for when combatting nutritional deficiencies.
33. Micha R, Mannar V, Afshin A, Allemandi L, Baker P, Battersby J *et al.*: *Global Nutrition Report: Action on Equity to End Malnutrition*. Bristol, UK: Development Initiatives; 2020.
 34. USDA US: *Department of Agriculture Agricultural Research Service*. Food Data Central; 2019.
 35. Abebe Y, Bogale A, Hambidge KM, Stoecker BJ, Bailey K, Gibson RS: **Phytate, zinc, iron and calcium content of selected raw and prepared foods consumed in rural Sidama, Southern Ethiopia, and implications for bioavailability.** *J Food Compos Anal* 2007, **20**:161-168.
 36. Yilmaz HO, Arslan M: **Teff: nutritional compounds and effects on human health.** *Acta Sci Med Sci* 2018, **2**:15-18.
 37. Gull A, Jan R, Nayik GA, Prasad K, Kumar P: **Significance of finger millet in nutrition, health and value added products: a review.** *Magnesium* 2014, **130**:120.
 38. Singh P, Raghuvanshi RS: **Finger millet for food and nutritional security.** *Afr J Food Sci* 2012, **6**:77-84.
 39. Renganathan VG, Vanniarajan C, Karthikeyan A, Ramalingam J: **Barnyard millet for food and nutritional security: current status and future research direction.** *Front Genet* 2020, **11**:500.
 40. Ugare R, Chimmad B, Naik R, Bharati P, Itagi S: **Glycemic index and significance of barnyard millet (*Echinochloa frumentaceae*) in type II diabetics.** *J Food Sci Technol* 2014, **51**:392-395.
 41. Davis KF, Chhatre A, Rao ND, Singh D, DeFries R: **Sensitivity of grain yields to historical climate variability in India.** *Environ Res Lett* 2019, **14**:064013
- A historical meta-analysis in India found that four millets were less sensitive to climate variation than the leading grain rice, and the authors propose that millet production can increase food security in India.
42. Abrouk M, Ahmed HI, Cubry P, Šimoníková D, Cauet S, Pailles Y *et al.*: **Fonio millet genome unlocks African orphan crop**

- diversity for agriculture in a changing climate. *Nat Commun* 2020, **11**:4488
- Genomics, population genetics, and breeding were used to identify the origin, genetic diversity, and selection of domestication genes related to seed shattering and yield in fonio millet. This approach can be used to identify targets to rapidly improve other millets.
43. Paterson AH, Bowers JE, Bruggmann R, Dubchak I, Grimwood J, Gundlach H *et al.*: **The *Sorghum bicolor* genome and the diversification of grasses.** *Nature* 2009, **457**:551-556.
 44. Bennetzen JL, Schmutz J, Wang H, Percifield R, Hawkins J, Pontaroli AC *et al.*: **Reference genome sequence of the model plant *Setaria*.** *Nat Biotechnol* 2012, **30**:555-561.
 45. Varshney RK, Shi C, Thudi M, Mariac C, Wallace J, Qi P *et al.*: **Pearl millet genome sequence provides a resource to improve agronomic traits in arid environments.** *Nat Biotechnol* 2017, **35**:969-976.
 46. Zou C, Li L, Miki D, Li D, Tang Q, Xiao L *et al.*: **The genome of broomcorn millet.** *Nat Commun* 2019, **10**:436.
 47. Hittalmani S, Mahesh HB, Shirke MD, Biradar H, Uday G, Aruna YR *et al.*: **Genome and transcriptome sequence of finger millet (*Eleusine coracana* (L.) Gaertn.) provides insights into drought tolerance and nutraceutical properties.** *BMC Genomics* 2017, **18**:465.
 48. VanBuren R, Man Wai C, Wang X, Pardo J, Yocca AE, Wang H *et al.*: **Exceptional subgenome stability and functional divergence in the allotetraploid Ethiopian cereal teff.** *Nat Commun* 2020, **11**:884.
 49. Serba DD, Muleta KT, St Amand P, Bernardo A, Bai G, Perumal R *et al.*: **Genetic diversity, population structure, and linkage disequilibrium of pearl millet.** *Plant Genome* 2019, **12**:1-12.
 50. Boyles RE, Brenton ZW, Kresovich S: **Genetic and genomic resources of sorghum to connect genotype with phenotype in contrasting environments.** *Plant J* 2019, **97**:19-39.
 51. Rajput SG, Santra DK: **Evaluation of genetic diversity of proso millet germplasm available in the United States using simple-sequence repeat markers.** *Crop Sci* 2016, **56**:2401-2409 <http://dx.doi.org/10.2135/cropsci2015.10.0644>.
 52. Lule D, de Villiers S, Fetene M, Odeny DA, Rathore A, Das RR *et al.*: **Genetic diversity and association mapping of Ethiopian and exotic finger millet accessions.** *Crop Pasture Sci* 2018, **69**:879 <http://dx.doi.org/10.1071/cp18175>.
 53. Puranik S, Sahu PP, Beynon S, Srivastava RK, Sehgal D, Ojulong H *et al.*: **Genome-wide association mapping and comparative genomics identifies genomic regions governing grain nutritional traits in finger millet (*Eleusine coracana* L. Gaertn.).** *Plants People Planet* 2020, **2**:649-662 <http://dx.doi.org/10.1002/ppp3.10120>.
 54. Diack O, Kanfany G, Gueye MC, Sy O, Fofana A, Tall H *et al.*: **GWAS unveils features between early- and late-flowering pearl millets.** *BMC Genomics* 2020, **21** <http://dx.doi.org/10.1186/s12864-020-07198-2>.
 55. Iohannes SD: **A Multidimensional Genomics Approach to Unfold the Ethiopian Teff (*Eragrostis tef*) Untapped Allelic Diversity and the Genomic Architecture of Adaptive Traits.** 2020.
 56. Boukail S, Macharia M, Miculan M, Masoni A, Calamai A, Palchetti E *et al.*: **Genome wide association study of agronomic and seed traits in a world collection of proso millet (*Panicum miliaceum* L.).** *BMC Plant Biol* 2021, **21**:330.
 57. Fahlgren N, Feldman M, Gehan MA, Wilson MS, Shyu C, Bryant DW *et al.*: **A versatile phenotyping system and analytics platform reveals diverse temporal responses to water availability in *Setaria*.** *Mol Plant* 2015, **8**:1520-1535 <http://dx.doi.org/10.1016/j.molp.2015.06.005>.
 58. Lacchini E, Kiegle E, Castellani M, Adam H, Jouannic S, Gregis V *et al.*: **CRISPR-mediated accelerated domestication of African rice landraces.** *PLoS One* 2020, **15**:e0229782
- CRISPR-Cas mediated genome engineering was used to modify key domestication loci to diminish lodging and improved seed size and yield in Kabre rice. This proof-of-concept study highlights how quickly key traits can be engineered in millets.
59. Peng R, Zhang B: **Foxtail millet: a new model for C₄ plants.** *Trends Plant Sci* 2021, **26**:199-201.
 60. Zsögön A, Čermák T, Naves ER, Notini MM, Edel KH, Weinl S *et al.*: **De novo domestication of wild tomato using genome editing.** *Nat Biotechnol* 2018, **36**:1211-1216 <http://dx.doi.org/10.1038/nbt.4272>.
 61. Sood P, Singh RK, Prasad M: **An efficient *Agrobacterium*-mediated genetic transformation method for foxtail millet (*Setaria italica* L.).** *Plant Cell Rep* 2020, **39**:511-525 <http://dx.doi.org/10.1007/s00299-019-02507-w>.
 62. Sood P, Prasad M: **Genetic transformation of *Setaria*: a new perspective.** *Compendium of Plant Genomes*. 2017:105-121 http://dx.doi.org/10.1007/978-3-319-65617-5_9.
 63. Mundada PS, Umdale SD, Ahire ML, Anil Kumar S, Nikam TD: **Transgenic finger millet [*Eleusine coracana* (L.) Gaertn.] for crop improvement.** *Genetically Modified Crops*. 2021:67-77 http://dx.doi.org/10.1007/978-981-15-5897-9_4.
 64. Sood P, Singh RK, Prasad M: **Millets genetic engineering: the progress made and prospects for the future.** *Plant Cell Tissue Organ Cult (PCTOC)* 2019, **137**:421-439 <http://dx.doi.org/10.1007/s11240-019-01587-6>.
 65. Bhatt R, Asopa PP, Jain R, Kothari-Chajer A, Kothari SL, Kachhwaha S: **Optimization of *Agrobacterium* mediated genetic transformation in *Paspalum scrobiculatum* L. (Kodo Millet).** *Agronomy* 2021, **11**:1104 <http://dx.doi.org/10.3390/agronomy11061104>.
 66. Lowe K, Wu E, Wang N, Hoerster G, Hastings C, Cho M-J *et al.*: **Morphogenic regulators *Baby Boom* and *Wuschel* improve monocot transformation.** *Plant Cell* 2016, **28**:1998-2015 <http://dx.doi.org/10.1105/tpc.16.00124>.
 67. Nelson-Vasilchik K, Hague J, Mookkan M, Zhang ZJ, Kausch A: **Transformation of recalcitrant sorghum varieties facilitated by *Baby Boom* and *Wuschel2*.** *Curr Protoc Plant Biol* 2018, **3**:e20076.
 68. Tian Z, Wang J-W, Li J, Han B: **Designing future crops: challenges and strategies for sustainable agriculture.** *Plant J* 2021, **105**:1165-1178
- This perspective highlights the future crops design project which aims to rapidly improve, or de novo domesticate alternative crops for increased food security.
69. Dagnaw H: **Influence of Nitrogen Fertilizer Rates and Varieties on Grain Yield, Grain Nutrition and Injera Sensory Quality of Tef [*Eragrostis tef* (Zucc.) Trotter] Varieties.** *Master's Thesis*. Addis Ababa, Ethiopia: Addis Ababa University; 2018.
 70. Pucher A, Sy O, Angarawai II, Gondah J, Zangre R, Ouedraogo M *et al.*: **Agro-morphological characterization of West and Central African pearl millet accessions.** *Crop Sci* 2015, **55**:737-748.
 71. Chandra AK, Chandora R, Sood S, Malhotra N: **Chapter 2 - global production, demand, and supply.** In *Millets and Pseudo Cereals*. Edited by Singh M, Sood S. Woodhead Publishing; 2021:7-18.
 72. Rao BD, Malleshi NG, Annor GA, Patil JV: **Millets Value Chain for Nutritional Security: A Replicable Success Model from India.** CAB; 2016.
 73. Chauhan M, Sonawane SK, Arya SS *et al.*: **Nutritional and nutraceutical properties of millets: a review.** *South Afr J Clin Nutr* 2018, **1**:1-10.
 74. Sanusi SN, Sulaiman SA, Bako HK: **Comparative of proximate and mineral composition of commercially-available millet types in Katsina Metropolis, Nigeria.** *World J Food Sci Technol* 2019, **3**:14-19.
 75. Ashoka P, Sunitha NH: **Review on browntop millet-a forgotten crop.** *J Exp Agric Int* 2020:54-60 <http://dx.doi.org/10.9734/jeai/2020/v42i730553>.
 76. Fern K, Fern A: **Useful Tropical Plants Database.** 2014 <http://tropical.theferns.info/>.
 77. Sood S, Khulbe RK, Gupta AK, Agrawal PK, Upadhyaya HD, Bhatt JC: **Barnyard millet - a potential food and feed crop of**

- future. *Plant Breed* 2015, **134**:135-147 <http://dx.doi.org/10.1111/pbr.12243>.
78. Anuradha N, Patro T, Triveni U, Rajkumar PJRS: **Trait association and genetic variability in browntop millet.** *J Pharmacogn Phytochem* 2020, **9**:1950-1953.
 79. Vetriventhan M, Upadhyaya HD: **Variability for productivity and nutritional traits in germplasm of kodo millet, an underutilized nutrient-rich climate smart crop.** *Crop Sci* 2019, **59**:1095-1106.
 80. Lin Z, Li X, Shannon LM, Yeh C-T, Wang ML, Bai G *et al.*: **Parallel domestication of the Shattering1 genes in cereals.** *Nat Genet* 2012, **44**:720-724.
 81. Konishi S, Izawa T, Lin SY, Ebana K, Fukuta Y, Sasaki T *et al.*: **An SNP caused loss of seed shattering during rice domestication.** *Science* 2006, **312**:1392-1396.
 82. Li C, Zhou A, Sang T: **Rice domestication by reducing shattering.** *Science* 2006, **311**:1936-1939.
 83. Wang E, Wang J, Zhu X, Hao W, Wang L, Li Q *et al.*: **Control of rice grain-filling and yield by a gene with a potential signature of domestication.** *Nat Genet* 2008, **40**:1370-1374.
 84. Ashikari M, Sakakibara H, Lin S, Yamamoto T, Takashi T, Nishimura A *et al.*: **Cytokinin oxidase regulates rice grain production.** *Science* 2005, **309**:741-745.
 85. Li M, Li X, Zhou Z, Wu P, Fang M, Pan X *et al.*: **Reassessment of the four yield-related genes Gn1a, DEP1, GS3, and IPA1 in rice using a CRISPR/Cas9 system.** *Front Plant Sci* 2016, **7** <http://dx.doi.org/10.3389/fpls.2016.00377>.
 86. Song X-J, Huang W, Shi M, Zhu M-Z, Lin H-X: **A QTL for rice grain width and weight encodes a previously unknown RING-type E3 ubiquitin ligase.** *Nat Genet* 2007, **39**:623-630.
 87. Xu R, Yang Y, Qin R, Li H, Qiu C, Li L *et al.*: **Rapid improvement of grain weight via highly efficient CRISPR/Cas9-mediated multiplex genome editing in rice.** *J Genet Genomics* 2016, **43**:529-532.
 88. Liu J, Chen J, Zheng X, Wu F, Lin Q, Heng Y *et al.*: **GW5 acts in the brassinosteroid signalling pathway to regulate grain width and weight in rice.** *Nat Plants* 2017, **3** <http://dx.doi.org/10.1038/nplants.2017.43>.
 89. Li Y, Fan C, Xing Y, Jiang Y, Luo L, Sun L *et al.*: **Natural variation in GS5 plays an important role in regulating grain size and yield in rice.** *Nat Genet* 2011, **43**:1266-1269.
 90. Doebley J, Stec A, Hubbard L: **The evolution of apical dominance in maize.** *Nature* 1997, **386**:485-488.
 91. Multani DS, Briggs SP, Chamberlin MA, Blakeslee JJ, Murphy AS, Johal GS: **Loss of an MDR transporter in compact stalks of maize br2 and sorghum dw3 mutants.** *Science* 2003, **302**:81-84.
 92. Jin J, Huang W, Gao J-P, Yang J, Shi M, Zhu M-Z *et al.*: **Genetic control of rice plant architecture under domestication.** *Nat Genet* 2008, **40**:1365-1369.
 93. Miura K, Ikeda M, Matsubara A, Song X-J, Ito M, Asano K *et al.*: **OsSPL14 promotes panicle branching and higher grain productivity in rice.** *Nat Genet* 2010, **42**:545-549.
 94. Huang X, Qian Q, Liu Z, Sun H, He S, Luo D *et al.*: **Natural variation at the DEP1 locus enhances grain yield in rice.** *Nat Genet* 2009, **41**:494-497.
 95. Asano K, Yamasaki M, Takuno S, Miura K, Katagiri S, Ito T *et al.*: **Artificial selection for a green revolution gene during japonica rice domestication.** *Proc Natl Acad Sci U S A* 2011, **108**:11034-11039.
 96. Li X, Qian Q, Fu Z, Wang Y, Xiong G, Zeng D *et al.*: **Control of tillering in rice.** *Nature* 2003, **422**:618-621.
 97. Pardo Jeremy, VanBuren Robert: **Evolutionary innovations driving abiotic stress tolerance in C4 grasses and cereals.** *Plant Cell* 2021, **11**:3391-3401 <http://dx.doi.org/10.1093/plcell/koab205>.