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Plant genetic resources for food and agriculture: novel materials for adapting to changing environmental conditions

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Abstract

Many present crop plants are in danger of failing due to extreme conditions induced by climate change. This along with a rapidly growing world population threatens global food security. In this paper, I provide an overview of different plant genetic resources, of possibilities to broaden their base by including crop wild relative species and other underutilized sources, and of conservation and characterization needs and tools. The increased environmental variability implies that we will need access to an even wider range of plant genetic resources than used today for breeding new crop varieties, which contain useful traits, such as pest and disease resistances and ability to withstand drought or extreme temperatures.

1. Introduction

Plant genetic resources provide the basis for sustainable agricultural production, adaptation to climate change and economic development. Besides being critical for food security, they are sources for energy, animal feed, fiber, ornamentals as well as other ecosystem services. Plant genetic diversity has an irreplaceable role as raw materials to improve the capacity of crops to adapt to climate change and other environmental challenges (Anderson et al., 2020; Henry, 2020). It is projected that a range of extreme events, such as heavy rains, floods, heat waves and droughts, will lead to changes in terrestrial ecosystems and place food security at risk, especially in the developing world (Ionesco et al., 2017; Anderson et al., 2020). IPCC (2014) estimates that some major agricultural crops may lose up to 25% of their present yield post 2050 due to climate change if better adapted crop varieties are not available. Furthermore, climate change-related events will be followed by losses in species density and diversity, changes in ecosystem composition resulting from novel species assortments, and declines in species not responding to climate change (Kovats et al., 2014; Harrison, 2020). Despite its recognized importance, plant biodiversity remains as a relatively poorly exploited source to support the breeding of crops adapted to new climates (Henry, 2020).

The present paper provides an overview of different types of plant genetic resources and their role as part of biodiversity, possibilities to widen the base of genetic resources by including crop wild relative species and other underutilized sources, conservation and characterization

needs and tools, and of the potential of discovering and utilizing novel genetic materials to respond to environmental challenges. The increased environmental variability that is expected to result from climate change implies that in future, farmers and plant breeders will need to be able to access an even wider range of plant genetic resources than today, while part of these genetic resources are also threatened by climate change and they must be protected (Kamenya et al., 2021). Many present crop plants may fail due to new extreme conditions induced by climate change (FAO, 2016). This, along with the rapidly growing world population, threatens global food security, for which solutions are urgent. Therefore, we should show a more proactive approach to climate adaptation, especially in species with a long lifespan, such as trees.

Biodiversity can be viewed at three levels, including the ecosystem, and taxonomic and genetic diversities (Coates et al., 2018). Of these, ecosystem diversity is the broadest. It is determined by the types of plants, animals, and microorganisms present, as well as by the physical characteristics and interactions (e.g., predator-prey relationships) of the region. Taxonomic diversity covers the number and abundance of species and other taxonomic units, e.g., subspecies in each area, while genetic diversity means genetic variation within and among populations of a species. Plant genetic resources are considered to include cultivars, landraces, crop wild relatives, ecotypes, and genetic stocks (Table 1). An unexpected situation concerning plant genetic resources is their underuse, not overexploitation that threatens their existence (Kamenya et al., 2021). If not being actively used, farmers'

Table 1. Types of plant genetic resources.

Type	Description
Cultivars	Varieties produced by plant breeders, usually uniform and adapted to high farm management standards
Landraces	Varieties developed over time in traditional farming systems, usually variable and adapted to local conditions
Crop wild relatives	Wild taxa within the same genus as a crop
Ecotypes	Populations of wild forms of domesticated species or their wild relative species, or other wild material; specific adaptations
Genetic stocks	Material undergone research or breeding programs resulting in specific information on a gene or character, or other data of value for breeding and research

crop varieties as well as those bred by professional plant breeders will not be maintained through continued selection. Rather, they will degrade and may eventually disappear. Yet, such currently underutilized crop plant materials may be able to contribute to climate adaptation and thus are certainly worth further research attention.

2. Widening the Base of Genetic Resources – Additional Options for Plant Breeding

Crop plants contain only a small part of all plant genetic diversity. However, certain wild plants, such as crop wild relatives (CWR), i.e., taxa related to crops that can possibly donate genes or alleles with potential beneficial traits and wild harvested plants, are an important part of biodiversity, carrying socio-economic value and enhancing food security (Maxted &

Kell, 2009; Fitzgerald et al., 2016; Hübner & Kantar, 2021). CWR genes have been used to improve many crops, e.g., wheat, maize, rice, barley, potato, cassava, and legumes (Dempewolf et al., 2017). Wild species carry useful traits, such as pest and disease resistances and ability to withstand waterlogging, drought, or extreme temperatures, and they can be used in breeding to improve nutritional value and to add much needed variation to crops (Dempewolf et al., 2017; Kamenya et al., 2021). As a result, the use of CWR genes may lead to a reduced application of pesticides, and sturdier plants which can better compete against weeds, thus reducing the use of herbicides. Enhanced drought-resistance can help save water by reducing irrigation need, plants with deeper rooting can improve soil stabilization, and those with a more effective use of nutrients demand less fertilizers.

In response to the increasing visibility and importance of CWRs in international political agendas since the early 1990's, numerous projects, tools and guidelines have been initiated and developed at local,

Table 2. Utility-based classification of plant germplasm resources according to Harlan and de Wet (1971).

Gene pool category	Description	Comments
Primary gene pool (GP-1)	<ul style="list-style-type: none"> •Crossing among individuals, normal seeds •Usually the same species 	•Gene transfer possible through routine breeding
Secondary gene pool (GP-2)	<ul style="list-style-type: none"> •Some barriers of crossability, often sterile hybrids •Usually closely related species 	•Special efforts needed to produce normal seeds
Tertiary gene pool (GP-3)	<ul style="list-style-type: none"> •Difficult to get hybrids, combinations often lethal or sterile •More distantly related species 	•Special methods: embryo culture, induced polyploidy or use of bridging crosses
Quaternary gene pool (GP-4)	<ul style="list-style-type: none"> •The extreme outer limit •Potentially all living organisms which contain DNA 	•More radical methods: protoplast fusion or genetic transformation

regional and global levels to enhance their use (Engels & Thormann, 2020). Furthermore, the application of technological advances in genomics, phenomics, biotechnology and data science can improve success in identifying and exploiting beneficial genetic variation in CWRs (Hübner & Kantar, 2021). Despite that, the genetic diversity of CWRs is still largely unknown. In addition, it is important to recognize that the ability to detect beneficial genetic variation in CWRs is strongly affected by the sampling plan, which should be designed according to the spatial and temporal variation of the target species, the trait of interest and the methods used (Hübner & Kantar, 2021). Until now, relatively little attention has been given to statistical, analytical and technical considerations that should guide CWR sampling, and germplasm characterization and use in breeding.

Major limitations of using CWRs in breeding are hybridization barriers

between undomesticated germplasm and the crop, which increases along with divergence (Viruel et al., 2020). Therefore, introducing CWRs into breeding programs is easier when the crop plant and CWR are closely related. A broad definition of a CWR would be any taxon belonging to the same genus as a crop (Maxted & Kell, 2009). However, applying this broad definition results in the inclusion of a very large number of species that may be closely or more remotely related to the crop plant. In addition, belonging to the same genus does not guarantee fertility among species, since taxonomic categories above the species level are arbitrary and may not reflect genetic relatedness satisfactorily. Therefore, knowledge of the evolutionary relationships is crucial and can be revealed with good resolution through DNA sequencing.

The gene pool concept is used to delineate the taxa that are CWR and then to identify levels of interfertility between

these taxa and the associated crop. An early and very influential system for recognizing gene pools was developed by Harlan and de Wet (1971) (Table 2). They proposed that the primary gene pool corresponds to a biological species including the crop and, therefore, individuals within the pool exhibit no barriers to reproduction. The secondary gene pool includes other taxa that could cross with the crop but with difficulty. Finally, they recognized the tertiary gene pool of taxa that are at the border of interfertility and could produce some anomalous seeds or could be utilized via special techniques, such as embryo culture. However, the quaternary gene pool is the extreme outer limit for breeding, including potentially all living organisms, which contain DNA. Breeding then requires genetic engineering methods, such as protoplast fusion or genetic transformation (Hübner & Kantar, 2021). A simple, often functional definition of a CWR would be a taxon found

within the primary or secondary gene pool of a crop, and between which gene exchange is relatively easy (Maxted et al., 2006).

Figure 1 illustrates the gene pool concept for the sunflower, *Helianthus annuus*, which is a relatively recent crop originating from North America. It has experienced a domestication bottleneck that has narrowed its genetic base, reducing it to 50–67% of the diversity present in the wild *H. annuus* populations (Kolkman et al., 2007; Mandel et al., 2011). However, the large number of *Helianthus* taxa (53 species) makes it possible to utilize a large genetic pool for crop improvement, such as enhanced resistances (Schilling, 2006; Stebbins et al., 2013). The primary gene pool (GP-1) consists of both cultivated and wild varieties of *H. annuus*, as well as of Winter's sunflower (*H. winteri*), a perennial species found in California (Stebbins et al., 2013; Seiler et al. 2017). It is easy for

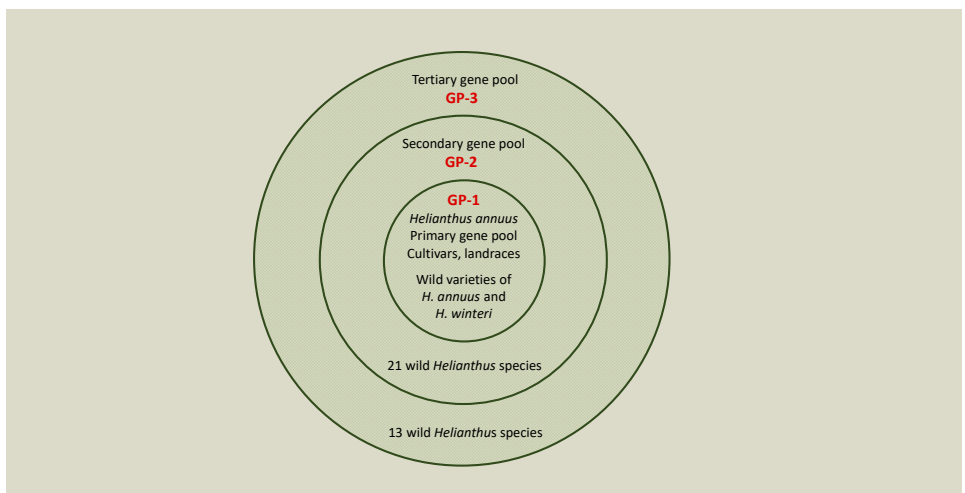


Figure 1. Gene pools of the sunflower (*Helianthus annuus*) illustrating the classification of plant germplasm resources according to Harlan and de Wet (1971), including primary (GP-1), secondary (GP-2) and tertiary gene pools (GP-3).

the genes of *H. winteri* to be brought into the cultivated sunflower. They could even be called different sub-species of the same species. The secondary gene pool (GP-2) is composed of 21 wild relatives that are different distinct species, but which are still so closely related that they can cross with the sunflower to at least some extent resulting in some fertile offspring (Kantar et al. 2015). The tertiary gene pool (GP-3) is composed of 13 more distantly related wild species that require specific breeding techniques to produce offspring (Kantar et al., 2015). All GP-2 and GP-3 *Helianthus* species possess traits of potential interest to sunflower breeding, especially those related to abiotic stress tolerance.

3. Conservation of Wild Genetic Materials for Crop Improvement

While great effort has been put into the collection and conservation of major crops, for many others considerable gaps remain, including CWRs. They are commonly not included in species conservation programs despite many of them being threatened or growing in threatened habitats; yet important progress in CWR conservation is emerging (Fitzgerald et al., 2016; Rubio Teso et al., 2021; Vincent et al., 2022). Conservation methods for wild plant genetic resources include *in situ* conservation in protected areas and *ex situ* conservation in gene banks. Main strategic elements needed in conserving genetic resources and utilizing them are the

following: emphasizing *in situ* conservation of diverse populations allowing evolution and generation of adaptive traits in the wild and expanding *ex situ* conservation by maintaining diversity and including populations from areas expected to be highly affected by climate change (FAO, 2012). *Ex situ* collections should contain genetic material adapted to environmental stresses, thereby contributing to climate change adaptation (Jarvis et al., 2015). Climate change will directly affect *in situ* conservation areas and new sites may be needed, if changing conditions do not support target populations in the future. Thus, it is important to take climate projections into account when selecting conservation sites.

A major effort to set the basis for an efficient conservation of the genetic diversity of priority CWR taxa in Europe, both *in situ* and *ex situ*, has been the recent work by the Farmer's Pride network, which has developed methodology, obtained novel results, and provided recommendations for CWR conservation (Rubio Teso et al., 2021). The main contributions included identifying priority CWRs for Europe and generating a database for them, estimating the genetic diversity of adaptive value present in each priority CWR using ecogeographic information as a proxy, and identifying sites where *in situ* genetic reserves of CWRs could potentially be established and *ex situ* collections maintained. An interesting approach has been to investigate the coincidence and degree of overlap between CWRs and biodiversity hotspots (Vincent et al., 2022).

4. Molecular Markers and Genomics in Germplasm Characterization and Breeding

Molecular marker techniques and DNA sequencing allow direct investigations of variation at the DNA level, thereby excluding all environmental influence. These analyses can be employed effectively, even at very early growth stages. Therefore, they have marginalized other methods in accession identification, diversity, and phylogenetic analyses, and when analyzing the genetic value of germplasm and conducting germ plasm selection, ultimately having an important impact on the development of more resilient varieties (Wambugu et al., 2018; Hübner & Kantar, 2021). With the development of these techniques, the amount of data available on genetic diversity has increased dramatically, leading to an improved understanding of issues such as domestication, adaptation, and genetic erosion. Applying genomic and other ‘omics’ analyses (i.e., analyses of complete genetic or molecular profiles of organisms based on genomics, transcriptomics, proteomics, or metabolomics), researchers can characterize the structure and function of genes, study plant development and responses to the environment, and understand speciation and the implications of diversity at the individual, population, and ecosystem levels. However, despite decreasing costs of generating molecular data, the expenses and work needed to reveal e.g., whole genome sequences of crops with large genomes, such as polyploid wheat, are still challenging and may hamper diversity

analyses and functional characterization (Adamski et al., 2020).

Molecular markers and genomics are finding wide application in the conservation and utilization of genetic resources and have the potential to revolutionize the way gene banks are managed. All crop improvement practices aim to capture genetic variants linked to desirable traits. The ability to accurately identify and track genome-wide genetic variation or individual molecular variants across generations of individuals offers a powerful tool for germplasm managers and plant breeders (Collard & Mackill, 2008; McCouch et al., 2012; Hübner & Kantar, 2021). For example, gene bank managers utilize molecular tools to establish and validate the identity of accessions in their collections, to determine genetic relationships among individuals and to perform gap analysis (i.e., evaluating the representation of biodiversity in conservation repositories such as gene banks) to guide collecting efforts (Hübner & Kantar, 2021). Moreover, extensive genotyping linked to measured traits allows the repositories of genetic resources to be searched for accessions carrying particular alleles or traits of interest.

Genomic selection has been associated with major performance gains in livestock species, and it has similar potential in plant species. Breeding programs use molecular genetic data to identify parents for crossing, to select offspring carrying desirable alleles in segregating populations, and to perform genomic prediction (e.g., Allier et al., 2019). A new genetic trait or combination of genetic characteristics could be designed and introduced into a cultivar to improve its qualities. Statistical models can be constructed to predict the

breeding value of an individual, given its genetic composition, and the optimal breeding scheme can be designed in the light of such predictions (Hübner & Kantar, 2021). Application of genomics for achieving greatly accelerated breeding for climate resilient, well-performing and better adapted crops requires a good understanding of the molecular and genetic basis of climate change adaptation (e.g., Wambugu et al., 2018). Conducting these kinds of studies requires long-term experiments or the availability of genetic resources, which have been collected from localities with varied climatic conditions and have thus been subjected to different climatic regimes over a long period of time. Novel alleles, which enhance adaptive capacity, should be prioritized for conservation, as they are important in developing climate resilient crops.

5. Novel or Underutilized Genetic Resources for Use: Examples

Landraces developed over time in traditional farming systems for numerous crop species are an underutilized source of genetic variation. One of these species is the common bean (*Phaseolus vulgaris*) that was domesticated in Mesoamerica and the Andes, but its secondary center of genetic diversity probably extended to Brazil, China, and Europe (Santalla et al., 2010). After domestication, this species has become one of the most important crop plants in developing countries. Jiménez and Korpelainen (2012, 2013) have

investigated the genetic diversity of Mesoamerican landraces of *P. vulgaris* and discovered a very high genetic diversity that is expected to allow adaptation to diverse environmental conditions, thus highlighting the potential of the local common bean germplasm for breeding purposes. The proper identification of these novel sources of genetic variation and their use in local breeding programs can justify and further enhance the conservation of locally adapted bean genetic resources in countries where a robust conservation strategy is still missing (Jiménez & Korpelainen, 2012). In addition, the utilization of wild relatives with specific adaptation traits, such as disease resistances, may be a useful addition to breeding programs.

Among palms, the date palm (*Phoenix dactylifera*) is the most widely cultivated species with a large number of cultivars. It has been the subject of intensive research (see, Elshibli & Korpelainen, 2011; Saboori et al., 2021). The date palm was also one of the first fruit trees to be domesticated around 6,800–6,300 BCE, followed by a complex history of breeding and use (Zohary & Hopf, 2000). Besides the date palm, there are other unexpected, yet potential palm genetic resources worth further investigation. For instance, the endangered, wild palm species *Medemia argun* occurs in the desert areas of Sudan and Egypt. It is highly tolerant to drought, which makes the species interesting as a production plant in areas exposed to extreme drought spells (Elshibli & Korpelainen, 2018). Its fruits are not palatable, and its presently known utilization possibilities are based on the use of its very strong fibrous leaves and woody stems for household and sheltering purposes. The

fruits of the related wild palm species *Hyphaene thebaica* and *Borassus aethiopum* are consumed, and it is believable that *M. argun* has a wider use potential than presently recognized. Elshibli and Korpelainen (2018, 2021) have investigated its population structure and genetic variability. The results show the genetic consequences of population fragmentation and the need of conservation actions to protect the *M. argun* palm with highly interesting adaptive traits.

Although beer production and the use of hop (*Humulus lupulus*) in the process are not as critical for food security as many other plant products, they are of a significant socioeconomical importance. There is evidence of beer brewing as early as 8,000 years ago in the Near East, and the process

Besides hop, there are many, yet marginally important herbs with considerable use potential.

was well known in Egypt and ancient Mesopotamia as early as c. 5000 BCE (Edwardson, 1952; Behre, 1999). Pollen records indicate that the Early Roman era (late years BCE) may be the period when the hop plants were first used in the brewing process (Edwardson, 1952; Wilson, 1975). There are presently a few hundred cultivated hop varieties, and new cultivars are being developed and tested

(Korpelainen & Pietiläinen, 2021). For instance, Eriksen et al. (2020) found cultivars that may be good candidates for growth in warm climates. Future hop breeding efforts with different quality and adaptation targets can utilize existing genetic resources, such as wild populations and landraces present in many regions. Climate change with higher temperatures and more frequent drought periods creates additional breeding needs. Novel genomic information being produced for the hop plant (Vergara et al., 2016; Padgitt-Cobb et al., 2021) will help in identifying unclear hop samples and finding cultivars that are both productive and resistant to stresses.

Besides hop, there are many, yet marginally important herbs with considerable use potential, for instance sorrels (genus *Rumex*). Sorrels have been utilized for thousands of years as food, herbal preparations and as a source of different colors of dyes (reviewed by Korpelainen & Pietiläinen, 2020). At the present, sorrels are mostly consumed through wild foraging or growing in home gardens. A few types of sorrel seeds are available commercially, including wild types and a few cultivars. The presence of high levels of oxalic acid lowers the bioavailability of some minerals, especially calcium, when uncooked parts of sorrel are consumed (Tuazon-Nartea & Savage, 2013). However, breeding effort could lead to developing different tasting varieties, along with lower oxalic acid contents. Many kinds of medicinal uses have been proposed (e.g., Vasasa et al., 2015). Yet, further investigations on different sorrel compounds are needed to provide scientific evidence for the medicinal effects of sorrel preparations. Sorrels are pseudometallophytes that have been found growing in several metal

contaminated sites and they are well adapted to acid mineral soils with a high availability of phytotoxic aluminum ions (Tolrà et al., 2005). The suggested applicability of sorrels for phytoremediation remains as a largely untouched research area. Altogether, sorrel is an underutilized plant that deserves more attention both in research and plant production. It is a multipurpose plant that has considerable potential as food and medicinal herb, and it can be grown in problem soils and used for phytoremediation.

6. Conclusions

Changing environmental conditions are a challenge for plant production and food security. Climate change is already negatively impacting agriculture, leading to reduced yields in some crops and regions. Without a sufficiently wide range of genetic resources, it will be difficult or even impossible to develop crops that will show sufficient resilience and adaptation in the future. Crop plants contain only a small part of all plant genetic diversity, but

the base of genetic resources can be widened by including crop wild relative species (CWR) and other underutilized sources. Especially CWRs contain a wide range of genetic diversity not present in cultivated crops, which can be used for breeding new adapted varieties. However, while great effort has been put in the collection and maintenance of genetic resources covering major crops, for many others, considerable gaps remain, including CWRs. In addition, CWRs are often poorly conserved, particularly *in situ*, and they are increasingly threatened in their natural habitats. This jeopardizes the use of CWRs as a source of genetic diversity for breeding new crop varieties, which contain useful traits, such as pest and disease resistances and the ability to withstand drought or extreme temperatures, and which can be used when breeding for improved nutritional value. The application of molecular genetic markers and genomics will accelerate breeding for climate resilient, well-performing and better adapted crops, thereby having a positive impact on global food and nutritional security.

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Photo: Veikko Somerpuro

References

- Adamski, N.M., Borrill, P., Brinton, J., Harrington, S.A., Marchal, C., Bentley, A.R., Bovill, W.D., Cattivelli, L., Cockram, J., Contreras-Moreira, B., Ford, B., Ghosh, S., Harwood, W., Hassani-Pak, K., Hayta, S., Hickey, L.T., Kanyuka, K., King, J., Maccaferri, M., Naamati, G., Pozniak, C.J., Ramirez-Gonzalez, R.H., Sansaloni, C., Trevaskis, B., Wingen, L.U., Wulff, B.B.H., & Uauy, C. (2020) A roadmap for gene functional characterisation in crops with large genomes: Lessons from polyploid wheat. *eLife* 9, e55646. <https://doi.org/10.7554/eLife.55646>
- Allier, A., Teyssèdre, S., Lehermeier, C., Charcosset, A., & Moreau, L. (2019). Genomic prediction with a maize collaborative panel: identification of genetic resources to enrich elite breeding programs. *Theoretical and Applied Genetics*, 133, 201–215. doi.org/10.1007/s00122-019-03451-9
- Anderson, R., Bayer, P.E., & Edwards, D. (2020). Climate change and the need for agricultural adaptation. *Current Opinion in Plant Biology*, 56, 197–202. doi.org/10.1016/j.pbi.2019.12.006
- Behre, K.-E. (1999). The history of beer additives in Europe - a review. *Vegetation History and Archaeobotany*, 8, 35–48. doi.org/10.1007/BF02042841
- David J. Coates, D.J., Byrne, M., & Moritz, C. (2018). Genetic diversity and conservation units: dealing with the species-population continuum in the age of genomics. *Frontiers in Ecology and Evolution*, 6, 165. doi.org/10.3389/fevo.2018.00165
- Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop Science*, 57, 1070–1082. doi.org/10.2135/cropsci2016.10.0885
- Edwardson, J.R. (1952). Hops—their botany, history, production and utilization. *Economic Botany*, 6, 160–175. doi.org/10.1007/BF02984875
- Elshibli, S., & Korpelainen, H. (2011). Biodiversity in date palm: molecular markers as indicators. In S.M. Jain, J. Al-Khayri & D.V. Johnson (Eds.), *Date Palm Biotechnology* (pp. 371–406). Dordrecht, Germany: Springer.
- Elshibli, S., & Korpelainen, H. (2018). Genetic profiling of the critically endangered palm species *Medemia argun* using newly developed chloroplast DNA markers. *Plant Ecology and Diversity*, 11, 185–192. doi.org/10.1080/17550874.2018.1455231
- Elshibli, S., & Korpelainen, H. (2021). Genetic diversity and population structure of *Medemia argun* (Mart.) Wurttenb. ex H.Wendl. based on genome-wide markers. *Frontiers in Ecology and Evolution*, 23. doi.org/10.3389/fevo.2021.687188
- Eriksen, R.L., Rutto, L.K., Dombrowski, J.E., & Henning, J.A. (2020). Photosynthetic activity of six hop (*Humulus lupulus* L.) cultivars under different temperature treatments. *HortScience*, 55, 403–409. doi.org/10.21273/HORTSCI14580
- Engels, J.M.M., & Thormann, I. (2020). Main challenges and actions needed to improve conservation and sustainable use of our crop wild relatives. *Plants*, 9, 968. doi.org/10.3390/plants9080968
- FAO (2012). *Second Global Plan of Action for Plant Genetic Resources for Food and Agriculture*. Rome, Italy: FAO.
- FAO (2014). *Nourishing people, nurturing the planet*. Rome, Italy: FAO.
- FAO (2016). *The State of Food and Agriculture: Climate Change, Agriculture and Food Security*. Rome: FAO.

- Fitzgerald, H., Korpelainen, H., & Veteläinen, M. (2016). Developing crop wild relative conservation strategy for Finland. In N. Maxted, E. Dulloo & B. Ford-Lloyd (Eds.). *Enhancing Crop Genepool Use: Capturing Wild Relative and Landrace Diversity for Crop Improvement* (pp. 206–216). Wallingford, UK: CABI.
- Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. *Philosophical Transactions of the Royal Society B*, 375. doi.org/10.1098/rstb.2019.0106
- Henry, R.J. (2020). Innovations in plant genetics adapting agriculture to climate change. *Current Opinion in Plant Biology*, 56, 168–173. doi:10.1016/j.pbi.2019.11.004
- Hübner, S., & Kantar M.B. (2021). Tapping diversity from the wild: from sampling to implementation. *Frontiers in Plant Science*, 12. doi:10.3389/fpls.2021.626565
- Ionesco, D., Mokhnacheva, D., & Gemenne F. (2017). *The Atlas of Environmental Migration*. New York: Routledge.
- IPCC (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.
- Jarvis, A., Upadhyaya, H., Gowda, C.L.L., Aggarwal, P.K., & Fujisaka, S. (2015). Plant genetic resources for food and agriculture and climate change. In *Coping with Climate Change, the Roles of Genetic Resources for Food and Agriculture* (pp. 9–21. Rome, Italy: FAO.
- Jiménez, O.R., & Korpelainen, H. (2012). Microsatellite markers reveal promising genetic diversity and seed trait associations in common bean landraces (*Phaseolus vulgaris* L.) from Nicaragua. *Plant Genetic Resources: Characterization and Utilization*, 10, 108–118. doi:10.1017/S1479262112000081
- Jiménez, O.R., & Korpelainen, H. (2013). Preliminary evaluation of F1 generation derived from two common bean landraces (*Phaseolus vulgaris*) from Nicaragua. *Plant Breeding*, 132, 205–210. doi.org/10.1111/pbr.12041
- Kamenya, S.N., Mikwa, E.O., Song, B., & Odeny, D.A. (2021). Genetics and breeding for climate change in Orphan crops. *Theoretical and Applied Genetics*, 134, 1787–1815. doi.org/10.1007/s00122-020-03755-1
- Kantar, M.B., Sosa, C.C., Khoury, C.K., Castañeda-Álvarez, N.P., Achicanoy, H.A., Bernau, V., Kane, N.C., Marek, L., Seiler, G., & Rieseberg L.H. (2015). Ecogeography and utility to plant breeding of the crop wild relatives of sunflower (*Helianthus annuus* L.). *Frontiers in Plant Science*, 6. doi.org/10.3389/fpls.2015.00841
- Kolkman, J.M., Berry, S.T., Leon, A.J., Slabaugh, M.B., Tang, S., Gao, W., Shintani, D.K., Burke, J.M., & Knapp, S.J. (2007). Single nucleotide polymorphisms and linkage disequilibrium in sunflower. *Genetics*, 177, 457–468. doi.org/10.1534/genetics.107.074054
- Korpelainen, H., & Pietiläinen, M. (2020). Sorrel (*Rumex acetosa* L.): not only a weed but a promising vegetable and medicinal plant. *Botanical Reviews*, 86, 234–246. doi.org/10.1007/s12229-020-09225-z
- Korpelainen, H., & Pietiläinen, M. (2021). Hop (*Humulus lupulus* L.): traditional and present use, and future potential. *Economic Botany*, doi.org/10.1007/s12231-021-09528-1
- Kovats, R.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., & Soussana, J.-F. (2014). Europe. In V.R. Barros, C.B. Field, D.J.

- Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White (Eds.), *Climate Change - Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1267–1326). Cambridge, UK: Cambridge University Press.
- Mandel, J.R., Dechaine, J.M., Marek, L.F., & Burke, J.M. (2011). Genetic diversity and population structure in cultivated sunflower and comparison to its wild progenitor *Helianthus annuus* L. *Theoretical and Applied Genetics*, 123, 693–704. doi: 10.1007/s00122-011-1619-3
- Maxted, N., Ford-Lloyd, B.V., Jury, S., Kell, S., Scholten, M. (2006). Towards a definition of a crop wild relative. *Biodiversity and Conservation*, 15, 2673–2685. doi.org/10.1007/s10531-005-5409-6
- Maxted N., & Kell S.P. (2009). *Establishment of a global network for the in situ conservation of crop wild relatives: Status and Needs*. Rome, Italy: FAO.
- Padgitt-Cobb, L.K., Kingan, S.B., Wells, J., Elser, J., Kronmiller, B., Moore, D., Concepcion, G., Peluso, P., Rank, D., Jaiswal, P., Henning, J., & Hendrix, D.A. (2021). A draft phased assembly of the diploid Cascade hop (*Humulus lupulus*) genome. *Plant Genome*, 14, e20072. doi.org/10.1002/tpg2.20072
- Rubio Teso, M.L., Álvarez Muñiz, C., Gaisberger, H., Kell, S.P., Lara-Romero, C., Magos Brehm, J., Maxted, N., Philips, J., & Iriondo, J.M. (2021). *European Crop Wild Relative Diversity: Towards the Development of a Complementary Conservation Strategy*. Birmingham, UK: University of Birmingham. Available at: D4.3_CWR_network_design.pdf.
- Saboori, S., Noormohammadi, Z., Sheidai, M., & Marashi, S. (2021). Insight into date palm diversity: genetic and morphological investigations. *Plant Molecular Biology Reporter*, 39, 137–145. doi.org/10.1007/s11105-020-01241-y
- Santalla, M., De Ron, A.M., & De La Fuente, M. (2010). Integration of genome and phenotypic scanning gives evidence of genetic structure in Mesoamerican common bean (*Phaseolus vulgaris* L.) landraces from the southwest of Europe. *Theoretical and Applied Genetics*, 120, 1635–1651. doi.org/10.1007/s00122-010-1282-0
- Seiler, G.J., Qi, L.L., & Marek, L.F. (2017). Utilization of sunflower crop wild relatives for cultivated sunflower improvement. *Crop Science*, 57, 1083–1101. doi.org/10.2135/cropsci2016.10.0856
- Schilling, E.E. (2006). *Helianthus*. In *Flora of North America Editorial Committee, Flora of North America North of Mexico*, 21, 141–169. New York and Oxford: Oxford University Press.
- Stebbins, J.C., Winchell, C.J., & Constable, J.V.H. (2013). *Helianthus winteri* (Asteraceae), a new perennial species from the southern Sierra Nevada foothills, California. *Aliso*, 31, 19–24. doi.org/10.5642/aliso.20133101.04
- Tolrà, R.P., Poschenrieder, C., Luppi, B., & Barcelo, J. (2005). Aluminium-induced changes in the profiles of both organic acids and phenolic substances underlie Al tolerance in *Rumex acetosa* L. *Environmental and Experimental Botany*, 54, 231–238. doi.org/10.1016/j.envexpbot.2004.07.006
- Tuazon-Nartea, J., & Savage, G. (2013). Investigation of oxalate levels in sorrel plant parts and sorrel-based products. *Food and Nutrition Sciences*, 4, 838–843. doi.org/10.4236/fns.2013.48109

- Vasas, A., Orbán-Gyupai, O., & Hohmann, J. (2015). The genus *Rumex*. Review of traditional uses, phytochemistry and pharmacology. *Journal of Ethnopharmacology*, 175, 198–228. doi.org/10.1016/j.jep.2015.09.001
-
- Vergara, D., White, K.H., Keepers, K.G., & Kane, N.C. (2016). The complete chloroplast genomes of *Cannabis sativa* and *Humulus lupulus*. *Mitochondrial DNA, Part A* 27, 3793–3794. doi.org/10.3109/19401736.2015.1079905
-
- Vincent, H., Hole, D., & Maxted, N. (2022). Congruence between global crop wild relative hotspots and biodiversity hotspots. *Biological Conservation*, 265. doi.org/10.1016/j.biocon.2021.109432.
-
- Viruel, J., Kantar, M.B., Gargiulo, R., Hesketh-Prichard, P., Leong, N., Cockel, C., Forest, F., Gravendeel, B., Pérez-Barrales, R., Leitch, I.J., & Wilkin, P. (2020). Crop wild phylorelatives (CWPs): phylogenetic distance, cytogenetic compatibility and breeding system data enable estimation of crop wild relative gene pool classification. *Botanical Journal of the Linnean Society*, 195, 1–33. doi.org/10.1093/botlinnean/boaa064
-
- Wambugu, P.W., Ndjiondjop, M.-N., & Henry, R.J. (2018). Role of genomics in promoting the utilization of plant genetic resources in genebanks. *Briefings in Functional Genomics*, 17, 198–206. doi.org/10.1093/bfgp/ely014
-
- Wilson, D.G. (1975). Plant remains from the Graveney boat and the early history of *Humulus lupulus* L. in W. Europe. *New Phytologist*, 75, 627–648. doi.org/10.1111/j.1469-8137.1975.tb01429.x
-
- Zohary, D., & Hopf, M. (2000). *Domestication of Plants in the Old World* (3rd edn). Oxford, UK: Oxford University Press.



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