A GLOBAL CONSERVATION STRATEGY FOR CROPS IN THE CUCURBITACEAE FAMILY

With support from

CROP TRUST

The International Treaty
ON PLANT GENETIC RESOURCES
FOR FOOD AND AGRICULTURE

**Federal Ministry
of Food
and Agriculture**

DISCLAIMER ABOUT THE ESTIMATED NUMBER OF ACCESSIONS PRESENTED IN THE STRATEGY AND CORRECTIONS MADE IN THIS SECOND VERSION OF THE STRATEGY

The number of accessions presented in the text and tables of this strategy are the best estimates the authors were able to make at the time of writing based on the data available and the methods used. Such estimates can differ depending on the sources of data and their completeness, the time of the analyses, and the assumptions made in carrying out the analyses. For example, estimates of the number of accessions of a specific taxon are often higher when integrating multiple data sources (e.g., FAO-WIEWS, Genesys and surveys) compared to using only one source. This is because using multiple sources allows the inclusion of some collections that are recorded in at least one data source but not all of them. Thus, an estimate of the number of *ex situ* accessions of a given taxon that integrates information from multiple sources should provide a more reliable estimate than an estimate using a single source. It should also be remembered that *ex situ* collections are not static and their size and composition can change through time. To avoid misinterpretation, comparisons of estimates done at different times, with different methods, and using different sources, should therefore be treated with caution. To minimize the likelihood of misinterpreting the estimates of number of accessions conserved *ex situ* presented in this document, the date of retrieval and the source(s) of the data are provided in each table. In this second version of the strategy we amended the captions of some tables to improve the accuracy of the date of retrieval of the data.

In this second version of the strategy, we dropped the term "unique" from some tables reporting the estimated number of accessions. In the footnotes, we previously explained that in these tables the phrase "unique accessions" refers to estimates after dropping only duplicates identified on the basis of the DONORNUMB and DONORCODE fields in passport data. A more accurate label would be "total accessions after dropping a limited number of duplicates identified on the basis of the DONORNUMB and DONORCODE fields in passport data." However, some colleagues were misled by the use of the label "unique accessions" and interpreted these figures as precise estimates of globally unique accessions. Rather, these are estimates of total global accessions after dropping only the most obvious duplicates. Most likely, they still include a large number of other unidentified duplicates.

At the time of writing this document, **the data available allowed to make fairly accurate estimates of global total accessions for the crops covered in this document. However, the authors did not have data allowing reliable estimates of globally <u>unique</u> accessions. Similarly, no data was available allowing estimates at global level of the percentage of accessions conserved *ex situ* that are <u>unique</u>.**

Supplementary material is available at https://doi.org/10.5281/zenodo.7712913. Any question about the strategy, and the data presented in the strategy, can be direct to peter.giovannini@croptrust.org

CONTENTS

APPENDICES

ACRONYMS

ABS	Access and Benefit Sharing
AEGIS	A European Genebank Integrated System
AVGRIS	Asian Vegetable Genetic Resources Information System
BGCI	Botanic Gardens Conservation International, UK
CAAS	Chinese Academy of Agricultural Sciences
CABYV	cucurbit aphid-borne yellow virus
CATIE	Tropical Agricultural Research and Higher Education Center
CENARGEN	National Center for Genetic Resources and Biotechnology, Brazil
CGMMV	cucumber green mottle mosaic virus
CGN	Centre for Genetic Resources, the Netherlands
CMV	cucumber mosaic virus
CNRG	Centro Nacional de Recursos Genéticos, Mexico
CRI	Crop Research Institute, Czech Republic
CSIC	Consejo Superior de Investigaciones Científicas, Spain
CSICELM	Consejo Superior de Investigaciones Científicas; Estación Experimental La Mayora, Spain
CucCAP	Cucurbit Coordinated Agricultural Project (USA)
CVYV	cucumber vein yellowing virus
CWR	crop wild relative
CYSDV	cucurbit yellow stunting disorder virus
DNA	deoxyribonucleic acid
ECCUDB	European Central Cucurbits Database
ECPGR	European Cooperative Programme for Crop Genetic Resources
EURISCO	European Search Catalogue for Plant Genetic Resources
FAO	Food and Agriculture Organization of the United Nations
GBIF	Global Biodiversity Information Facility
GeRRI	Genetic Resources Research Institute, Kenya
GRIN	Germplasm Resources Information Network
GRSU	Genetic Resources and Seed Unit (WorldVeg)
GWAS	genome-wide association study
ICAR	Indian Council of Agricultural Research
ICARDA	International Center for Agricultural Research in the Dry Areas
ICBA	International Center for Biosaline Agriculture, United Arab Emirates
ILRI	International Livestock Research Institute
INIFAP	Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Mexico
IPGR	Institute of Plant Genetic Resources, Bulgaria
IPK	Institut für Pflanzengenetik und Kulturpflanzenforschung, Germany

ISTA	International Seed Testing Association
ITPGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
Ma	million years ago
MNSV	melon necrotic spot virus
MS	Microsoft
MTA	Material Transfer Agreement
MYSV	melon yellow spot virus
NARO	National Agriculture and Food Research Organization, Japan
NBPGR	National Bureau of Plant Genetic Resources, India
NordGen	Nordic Genetic Resource Center
NPGRC	National Plant Genetic Resources Centre, Botswana
NPGRL	National Plant Genetic Resources Laboratory, Philippines
NPGS	National Plant Germplasm System, USA
PGR	plant genetic resources
PRSV	papaya ringspot virus
RH	relative humidity
QMS	quality management system
QTL	quantitative trait locus
SADC	Southern African Development Community
SINAREFI	Sistema Nacional de Recursos Fitogenéticos, Mexico
SMTA	Standard Material Transfer Agreement
SNICS	Sistema Nacional de Inspección y Certificación de Semillas, Mexico
SNP	single nucleotide polymorphism
SSR	simple sequence repeat
ToLCNDV	tomato leaf curl New Delhi virus
TYLCThV	tomato yellow leaf curl Thailand virus
UNAM	Universidad Nacional Autónoma de México
UPOV	International Union for the Protection of New Varieties of Plants
USDA	United States Department of Agriculture
UzRIPI	Uzbek Research Institute of Plant Industry, Uzbekistan
VIR	N. I. Vavilov Institute of Plant Genetic Resources, Russia
WBNV	watermelon bud necrosis virus
WG	Working Group
WIEWS	World Information and Early Warning System
WMV	watermelon mosaic virus
WorldVeg	World Vegetable Center
WSMoV	watermelon silver mottle virus
ZYMV	zucchini yellow mosaic virus

EXECUTIVE SUMMARY

Background: As part of a new initiative led by the Global Crop Diversity Trust (the Crop Trust), a conservation strategy has been developed for crops in the Cucurbitaceae family. The strategy provides background information (e.g., agronomic, cultural and economic importance) for a variety of economically important Cucurbitaceae crops, as well as an overview of each crop and its wild relatives (CWRs). The strategy briefly discusses the origins, domestication and centers of crop genetic diversity, highlighting important CWRs, and provides up-to-date information on crop taxonomy and gene pools. Importantly, current *ex situ* holdings for the major crops are summarized, indicating vulnerabilities (particularly for landraces and CWRs) and gaps in existing collections. Within the strategy, survey data collected from genebanks with Cucurbitaceae collections inform a discussion of current germplasm and genebank management, highlighting research gaps and outlining ways to improve the efficiency and effectiveness of crop genetic diversity conservation. The content of the strategy is derived from a thorough literature review combined with four activities sponsored by the Crop Trust: (i) an expert meeting at the Crop Trust in Bonn, Germany (October 2019); (ii) an expert consultation workshop in Thailand (December 2019); (iii) a detailed online survey sent to 50 genebanks around the world; (iv) analysis of data from Genesys, WIEWS and other online germplasm databases.

Aim: The strategy aims to promote the rationalization of conservation efforts at national, regional and global scales, and to identify priority actions to strengthen the conservation of cucurbit genetic resources. Approaches include encouraging partnerships and the sharing of responsibilities, facilities and tasks for the conservation and sustainable use of Cucurbitaceae crop genetic resources. The document is intended to lead to strong stakeholder engagement and community ownership.

Taxonomy and taxa considered: The Cucurbitaceae family comprises roughly 95 extant genera and close to 1,000 species. About 90% of the species in the family are found in tropical and subtropical regions worldwide, mainly in Africa and Madagascar, Mesoamerica and South America, and South and Southeast Asia. Within the family, there are several major crops of worldwide economic importance, as well as many other crops of regional importance. Crops from three genera, *Citrullus* (watermelon), *Cucumis* (cucumbers, melons) and *Cucurbita* (pumpkins, squash), rank among the top 10 fruit/vegetable crops globally, in terms of economic importance.

The genus ***Cucumis*** contains two major crops: cucumber (*C. sativus*) and muskmelon (*C. melo*). In 2018, Asia accounted for 88% of global cucumber and gherkin production, with China alone producing 75% of world output. Similarly, for muskmelon, most production in 2018 occurred in Asia (73%), with China again accounting for the greatest share (47%). Asia is the ancestral area for the most recent common ancestor of melon and cucumber, which both have

progenitor populations in the Himalayan region. Recent evidence suggests a second, independent domestication of *C. melo* in Africa.

The genus **Citrullus** includes only seven species, of which four are regularly cultivated. These are the major global crop *C. lanatus* (dessert watermelon) and three minor crops of more regional importance: *C. amarus* (citron melon), *C. colocynthis* (colocynth) and *C. mucosospermus* (egusi melon, cultivated for its nutritious seeds). After cucumber, watermelon is the second most economically important crop of the Cucurbitaceae, and it also ranks second only to banana among the primary fruit crops in terms of production. China is by far the largest watermelon producer, responsible for 61% of global production in 2018. The exact origins of *C. lanatus* remain under debate, but northeastern Africa is currently thought to be the most likely center of origin. The other culti-vated *Citrullus* species are also African in origin.

The genus **Cucurbita** is native to the Americas but has been widely cultivated in other parts of the world since the 1500s. Of the 15 *Cucurbita* species, five are regularly cultivated: *C. argyrosperma* (cushaw), *C. ficifolia* (fig-leaf gourd), *C. maxima* (pumpkin/winter squash), *C. moschata* (butternut squash) and *C. pepo* (summer squash). *Cucurbita* crop species rank among the world's earliest domesticates; for example, the initial domestication of *C. pepo* occurred 8,000–10,000 years ago in present-day Mexico. Today, Mexico remains a center of diversity for wild *Cucurbita* species, which are found from midwestern USA to southern Argentina.

Other major global crops are found in the following genera: *Benincasa*, *Lagenaria*, *Luffa* and *Momordica*.
- **Benincasa hispida** (wax gourd) is an important crop in China and countries in Southeast Asia. Similar morphologically to the *Cucurbita*, wax gourd is cultivated for its large, edible fruits. The domestica-tion history of wax gourd remains unclear, but it is presumably a very ancient crop.
- **Lagenaria siceraria** (bottle gourd) is also an ancient crop, with a unique history of natural transoceanic dispersal from its native Africa. Domesticated inde-pendently in two very different parts of the world, East Asia and the Americas, mature bottle gourds are prized as watertight containers.
- Out of eight **Luffa** species, two are regularly cultivated in tropical regions worldwide, and are of economic importance in South and Southeast Asia: *L. acutangula* (angled loofah) and *L. cylindrica* (smooth loofah). While their immature fruits are edible, loofah fruits are most widely appreciated

when mature for their structural properties, as the dried fruits form natural sponges.
- The genus **Momordica** comprises nearly 60 spe-cies distributed across Africa (where the genus originated), Asia and Australia. Within the genus, there is one major global crop, *M. charantia* (bitter gourd), as well as three minor crops of regional importance: *M. balsamina* (balsam apple), *M. cochinchinensis* (gac) and *M. dioica* (spiny gourd). Bitter gourd is extensively cultivated in South and Southeast Asia for its immature, bitter fruits.

Cucurbit crops of more regional economic impor-tance are found in three additional genera: *Coccinia*, *Sechium* and *Trichosanthes*.
- The perennial vine **Coccinia grandis** (ivy gourd) is native to East Africa, but is now a crop of regional importance in Southeast Asia and in India, where it has been used for centuries in traditional medicine. High in carotenoids, ivy gourd is also an important source of vitamin A in developing countries. Only partially domesticated, *C. grandis* spreads vegeta-tively and can be invasive.
- Mexico has been identified as the ancestral area of the clade containing **Sechium**. Within the genus are two cultivated species: *S. edule* (chayote), which is grown in subtropical and tropical regions worldwide, and *S. tacaco*, which is cultivated only in Costa Rica. The largest producers of chayote are Mexico and Costa Rica.
- **Trichosanthes** is the largest genus in the Cucurbi-taceae family. Its center of diversity is in Southeast Asia, with *Trichosanthes* species found from India to Japan and southeast to Australia and Fiji. Within the genus are two cultivated species, *T. cucumerina* (snake gourd) and *T. dioica* (pointed gourd), both widely cultivated in tropical regions for their imma-ture fruits.

Most wild cucurbits produce highly bitter fruits, due to high concentrations of toxic chemicals called cucur-bitacins. These compounds are present not only in the fruits of wild cucurbits, but also in their leaves and roots, where they play an important role in herbivory deterrence. The bitterness of most Cucurbitaceae fruit crops has decreased during domestication, with the exception of bitter gourd (*M. charantia*), in which bitterness has been selectively retained. In addition, some crops (e.g., muskmelon and watermelon) have also undergone selection for increased sugar content during domestication.

Conservation status: For the most economically important Cucurbitaceae genera (i.e., *Citrullus*, *Cucumis* and *Cucurbita*), data were collated from the

World Information and Early Warning System (WIEWS; hosted by FAO), Genesys, the USDA-GRIN database and the strategy survey to characterize *ex situ* collections of these genera, including the number of accessions and their location. Following is a summary of the results.

For *Citrullus*, a genus native to Africa, there are 13,856 accessions worldwide, held in 91 institutes. Of these, 49% are held in four genebanks: RUS001, USA016, BRA017 and JPN183. North Africa, West Africa, Central and East Africa, and South America should be targeted for additional collecting. Regarding *Citrullus* CWRs, there are fewer than 10 accessions of *C. ecirrhosus* and *C. rehmii* and only two accessions of *C. naudinianus* in *ex situ* collections.

There are 35,655 accessions of *Cucurbita* worldwide, held in 127 institutes. Of these, 35% are held in six genebanks: RUS001, BRA012, CRI001, CHN001, BRA003 and USA016. *Cucurbita moschata* has the highest number of accessions conserved *ex situ*, followed by *C. pepo* and *C. maxima*. *Cucurbita* CWRs are mainly conserved in a few institutes (BRA003, USA020, USA016, CZE122, JPN183 and MEX208). Among *Cucurbita* CWRs, *C. cordata*, *C. pedatifolia*, *C. radicans* and *C. x scabridifolia* are high priority for further collecting, followed by *C. digitata*, *C. foetidissima* and *C. palmata*. For *Cucurbita argyrosperma* subsp. *argyrosperma*, further collecting of landraces in Central America and duplication of collections at risk should be a priority. For *C. moschata*, germplasm from Colombia is underrepresented *ex situ*, and, generally, the primary center of diversity (Mexico, Central America and northern South America) is better represented *ex situ* than secondary centers of diversity (Asia).

There are 39,296 accessions of *Cucumis* worldwide, held in 121 institutes. Of these, 41% are held in three genebanks: RUS001, USA020 and JPN183. *Cucumis melo* has the highest number of accessions conserved *ex situ*, followed by *C. sativus*. *Cucumis anguria* and *C. metuliferus* have relatively low numbers of accessions conserved *ex situ*. Germplasm of African origin for *C. melo* and *C. sativus* is underrepresented in *ex situ* collections. Furthermore, there are no records of accessions for *C. picrocarpus*, the closest CWR of *C. melo*.

For all the genera considered in this strategy, a large proportion of collections have unknown biological status. This constitutes a major issue that confounds the interpretation of the composition of published/reported *ex situ* Cucurbitaceae germplasm holdings around the globe.

For several other Cucurbitaceae genera containing major crops, data were collated from WIEWS, Genesys, USDA-GRIN and the strategy survey, as follows:

	Number of accessions	Largest germplasm collections
Benincasa	1,650	World Vegetable Center (WorldVeg) (315); national genebanks in China (300), India (270), Bangladesh (323)
Lagenaria	5,731	National genebanks in the USA (900), India (743), Kenya (478), China (370), South Africa (350); WorldVeg (346)
Luffa	3,279	WorldVeg (871); national genebanks in Bangladesh (833), India (701), USA (169), Brazil (144)
Momordica	3,026	National genebanks in Bangladesh (814), India (584), Japan (383), China (200); WorldVeg (622)

Participants from Africa, the Americas and Asia who attended the expert consultation workshop for this strategy, held in Thailand in December 2019, reported accelerated losses of genetic diversity for Cucurbitaceae crop species due to urbanization, deforestation, changes in agricultural practices and changes in food consumption habits. For example, the genetic diversity of wild *Cucurbita* species in the USA is decreasing due to habitat loss, and the cultivation of genetically modified squashes (e.g., virus-resistant *Cucurbita pepo*) in Mexico and the USA is also a potential threat to wild *C. pepo* populations, owing to the high risk of hybridization. Of the CWRs, *Cucurbita radicans* has been assessed as globally endangered, while *C. okeechobeensis* subsp. *okeechobeensis* is nearly extinct; other *Cucurbita* wild relatives are rare. Furthermore, *Cucurbita ex situ* germplasm collections conserved at INIFAP and SINAREFI, Mexico (Xitlali Aguirre-Dugua, personal communication, expert consultation workshop Thailand, 11–13 Dec. 2019) are severely threatened and rapidly losing viability.

Concerning genebank and germplasm management, participants in the expert consultation meeting stressed that there is a need to improve passport data; in particular, the registration of donor data for accessions introduced from other genebanks is needed in order to assist in the identification of unique accessions. Best-practice regeneration protocols for Cucurbitaceae crops should be shared and harmonized. There is also a need to adopt germplasm management systems that follow internationally agreed genebank standards. Although descriptor lists exist for major crops of the Cucurbitaceae family, they are yet to be standardized or developed for minor crops.

An online survey of Cucurbitaceae collections revealed that 68% of genebanks (17 out of 25 respondents) felt that species coverage of the Cucurbitaceae germplasm conserved *ex situ* is insufficient. A further 56% of respondents highlighted insufficient ecological representation of the species conserved, while 44% noted that population (sample) representation per species is inadequate. It is important to fill collection gaps for wild relatives in the Americas, Africa and Asia and for landraces in primary regions of diversity (e.g., Mexico), as well as other regions with unique genetic diversity (e.g., Myanmar, Bangladesh and China). Collections from extreme environments might also be prioritized to capture abiotic stress tolerances, and from areas with high pest and disease pressures to identify genotypes presenting single or multiple resistance.

Breeding: The narrow genetic base of many cucurbit crop cultivars is a major challenge for breeders aiming to develop improved varieties with both abiotic and biotic stress resistance. Crop wild relatives and landraces may serve as sources of such genetic diversity and must be conserved *ex situ*. Improved technologies, especially genomics-assisted breeding, are facilitating the introgression of favorable traits from wild species into cultivars. To expedite the use of conserved diversity in breeding programs, the full characterization of genebank collections is necessary. Mobilization of broad crop gene pool diversity will allow breeders to develop resistant cultivars adapted to rapidly changing environmental conditions, thus boosting agricultural production and ensuring food and nutritional security.

Seed viability: The Cucurbitaceae survey revealed that seed viability monitoring varies among genebanks, ranging from 5 to 25 years. Predicting the seed lifespan of the wide range of Cucurbitaceae species is a major challenge for most genebanks. Seeds may unexpectedly die during storage, potentially leading to accession loss over time. Seed longevity is determined by both internal seed traits and storage conditions (e.g., humidity, temperature, oxygen levels). Seed traits are influenced by gene–environment interactions during seed maturation and harvest. Interactions between these factors are believed to contribute to the wide variation observed within and among species and seed lots. Enhancing the seed lifespan of Cucurbitaceae seeds should be a major focus of future research, especially for the genus *Momordica*, whose seeds lose viability rapidly at subzero temperatures.

Seed health: Seedborne diseases in the Cucurbitaceae are a major concern for the safe movement of germplasm across borders, currently presenting a significant challenge for genebanks that distribute germplasm internationally. As it is technically difficult and expensive for individual genebanks to invest in indexing, testing and certifying germplasm health, the designation of regional third-party providers to undertake these tasks may improve cost-efficiency and reliability. The development of chemical or temperature seed treatments for disease-free cucurbit germplasm and research on their impact on seed longevity should be a priority for collaborative research on cucurbit conservation and germplasm exchange.

Regeneration: Compared to other crop species, the availability of cucurbit accessions for distribution is relatively modest, especially for CWRs. This may be due, at least in part, to challenges with regeneration, as well as to the relatively short shelf life of some species, such as bitter gourd, and wild taxa under orthodox seed storage conditions. The result of a search in Kew Seed Information Database (Royal Botanic Gardens Kew, 2020) for the genera *Cucurbita*, *Citrullus*, *Cucumis*, *Momordica*, *Luffa*, *Benincasa* and *Lagenaria* indicated that all the taxa of these genera where storage behavior is known have orthodox storage behavior. However, this has not been the practical experience of many genebanks, which have faced significant challenges conserving *Momordica* germplasm.

Regeneration is costly and technically challenging in the Cucurbitaceae as most species are allogamous and require hand or bee pollination, and photoperiod sensitivity may also limit regeneration success. In general, regeneration backlogs threaten the security and availability of conserved materials in a majority of genebanks. Regeneration backlogs might be addressed through collaborations among genebanks, with those having spare capacity and suitable environmental conditions for regeneration assisting those with backlogs; collaborations with private seed companies may also be beneficial. Further studies of seed longevity to enhance long-term viability in storage could reduce conservation costs by decreasing regeneration frequency.

International policies: The Nagoya Protocol, a supplementary agreement to the Convention on Biological Diversity, was described as an obstacle to the accessibility and distribution of Cucurbitaceae germplasm. Participants in the expert consultation workshop stressed the need to expand the list of Annex I crops covered by the Multilateral System of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) to include Cucurbitaceae crops; this would greatly facilitate germplasm exchange. For the global Cucurbitaceae community, stronger connections (i.e., to exchange both information and germplasm) are desired with genebanks that hold large cucurbit collections, such as those of China, Japan and Russia (VIR).

Documentation: Many national genebanks still lack adequate germplasm documentation and information systems, disconnecting them from the international plant genetic resources community and potential germplasm users. Those genebanks should be assisted through the adoption of proven documentation systems, such as GRIN-Global. Once collection information is electronically captured in a standard format, it can then be easily added to global databases (e.g., Genesys and WIEWS) to encourage and facilitate germplasm distribution and use.

International collaboration: To strengthen collaboration among genebanks, the European Cooperative Programme for Plant Genetic Resources (ECPGR) may serve as a good example. Under the ECPGR, the European Search Catalogue for Plant Genetic Resources (EURISCO) was created, initially focusing on accession-level passport data. More recently, characterization and evaluation data have also been included for the benefit of germplasm users. EURISCO communicates with Genesys, a global PGR database. Greater collaboration with the Cucurbitaceae community, following the ECPGR model, for example, will improve the security of cucurbit conservation and enable more sustainable use of cucurbit PGR.

Conclusions: A global conservation system for Cucurbitaceae genetic resources should be **comprehensive**, **secure**, **efficient** and **cost-effective**, with germplasm and detailed **accession-level information easily accessible**, ideally in centralized global databases such as Genesys.

A strategy to achieve such a system should include the following elements:
- Regeneration of threatened genebank accessions (e.g., due to low seed stocks, poor seed quality, or seed health problems).
- Revision and harmonization of international, regional and national genebank databases: update the availability of cucurbit genetic resources and compare matching and non-matching accessions based on passport, morphological and molecular information.
- Collecting from priority areas to fill gaps in existing collections: for wild relatives, in the Americas, Africa and Asia; for landraces, in primary regions of diversity (Mexico, Myanmar, Bangladesh and China).
- Regional collaboration to safeguard unique landraces and CWRs held by national genebanks but not yet duplicated in regional or international genebanks; for example: in Africa, at the SADC Plant Genetic Resources Centre Genebank Network for Southern Africa and the World Vegetable Center (WorldVeg) genebank in Tanzania; in the Americas, at the USDA National Plant Germplasm System (USDA NPGS); in Europe, at genebanks with key cucurbit collections, such as the Centre for Genetic Resources, the Netherlands (CGN); and in Asia and Oceania, at the WorldVeg genebank. Regional genebanks must commit to providing materials to national genebanks upon request.
- Support for national programs that conserve accessions under medium-security conditions and perform germplasm evaluation.
- Commitment by regional genebanks to meeting policy and phytosanitary requirements for international exchange of Cucurbitaceae germplasm under the terms of the ITPGRFA and/or Nagoya Protocol.
- Development of seed health protocols for the safe distribution of Cucurbitaceae germplasm to avoid the introduction and dispersal of seedborne pathogens. Designation of regional third-party providers to undertake phytosanitary tasks in a cost-efficient and standardized way.
- Periodic capacity building to equip national collections with trained and capable personnel.

Cucumis melo subsp. *melo*: one opened fruit and many fruits under cultivation. Chromolithograph, c. 1890. Source: Wellcome Collection

1 INTRODUCTION AND STRATEGY BACKGROUND

1.1 Context and precedents

The Crop Trust is supporting efforts to develop global crop conservation strategies for the efficient and effective conservation of crop diversity, particularly in *ex situ* collections. The effort is supported by the Government of Germany. These strategies describe the current conservation status of major collections, and attempt to identify priority activities and resources required to safeguard crop diversity. Currently, conservation strategies exist for 26 crops; these were developed on behalf of the Crop Trust and its partners. In addition, a conservation strategy for cacao was developed by Bioversity International in September 2012. The development of the crop conservation strategies spans a period of 12 years, with the first, for potato, published in 2006 and the most recent, for tea, in 2019. In addition, a set of regional strategies were developed for the Americas; Central Asia and the Caucasus; East Africa; the Pacific Islands; South, Southeast and East Asia; Southern Africa; West Asia and North Africa; and West and Central Africa (Khoury et al. 2010).

The Global Crop Diversity Trust's global crop conservation strategies share a set of common goals, as follows:
- To review the history of crop collections and identify where unique materials are held
- To assess the challenges faced by crops and their genetic resources
- To provide guiding documents for the development of a rational global system for *ex situ* conservation
- To provide in-depth crop-specific assessments and information, fully complementary to FAO's Global Plan of Action and State of the World reports.

A typical global crop conservation strategy contains three major elements, as follows:
1. Background information on the origins and diversification, current economic importance, biology, agronomy, breeding and production of a crop
2. Overview of existing *ex situ* collections (holding landraces, obsolete improved varieties, advanced improved cultivars, breeding/research materials, genetic stocks and crop wild relatives) including institutional and organizational setups
3. Assessment of threats/challenges to *ex situ* conservation of crop genetic resources and suggestions for how to rationalize and increase efficacy of conservation and use (including documentation, regeneration, distribution, safety back-up, gap filling, etc.).

In the context of a new project called *Breathing New Life into the Global Crop Conservation Strategies: Providing an Evidence Base for the Global System of* Ex Situ *Conservation of Crop Diversity*, funded by the German Government, the Crop Trust began an initiative to revise and update some of the existing 26 crop strategies, as well as to develop a number of new strategies, including one for the Cucurbitaceae (Appendix I and II). The present strategy will promote the rationalization of conservation efforts at national, regional and global levels, for example by encouraging partnerships and the sharing of responsibilities, facilities and tasks for the conservation, enhancement and sustainable use of Cucurbitaceae crop genetic resources.

1.2 Information sources

The principal sources of information for the Cucurbitaceae strategy include a detailed online survey sent to the curators and/or genebank managers of 50 genebanks around the world known to conserve Cucurbitaceae germplasm (Appendix III); a consultation workshop of crop experts and cucurbit curators/genebank managers held at the Regional Office/Training Center of WorldVeg at Kamphaeng Saen, Kasetsart University, Thailand, on 11–13 December 2019 (Appendix IV and V); the WIEWS and Genesys germplasm databases; GRIN-NGPS (for taxonomical information and data on USDA accessions; the Plant Search database of the Botanic Gardens Conservation International (BGCI), the Plant List and the Global Biodiversity Information Facility (GBIF); gap analyses for crop wild relatives (CWRs) and landraces; recent literature; and the personal contacts and experience of the strategy author and editors.

The online survey (Appendix VI) was sent to potential respondents on 23 October 2019 and closed on 2 December 2019. Out of the 50 survey requests, 28 responses were received during this period, a response rate of 56%. The respondents represented genebanks in:
- **Africa**: Malawi (1 institution), Tanzania (1)
- **Americas**: Argentina (1), Brazil (3), Chile (1), Costa Rica (1; regional genebank), USA (5)
- **Asia/Oceania:** China (1), India (1), Japan (1), Uzbekistan (1)
- **Europe:** Czech Republic (1), Germany (1), Netherlands (1), Poland (1), Portugal (1), Romania (1), Russia (1), Spain (1), Sweden (1), Switzerland (1)
- International: 1

2 CROP BACKGROUND

The Cucurbitaceae family, commonly known as the gourd family, comprises some 965 tropical and subtropical species collectively known as "cucurbits" (Christenhusz and Byng 2016; Schaffer and Paris 2016). Family members are distinguished by their tendril-bearing vines (Renner and Schaefer 2017) and characteristic fruits (Lebeda et al. 2007), which are a kind of modified berry, called a "pepo." The fruits are remarkably variable, both across and within species, ranging strikingly in size, shape and color; many are consumed as fruits or vegetables, and play an important role in human nutrition. In fact, though the Cucurbitaceae family is not particularly large (compared to other vascular plant families; Willis et al. 2017), it contains a high proportion of economically important species, including some of the world's earliest domesticates (Lira-Saade 1995). Cucurbit species from at least 20 genera are grown for culinary purposes, medicinal applications and as ornamentals (Schaffer and Paris 2016), among other purposes (e.g., for use as containers, or as structural materials in other products). The most widely grown and globally valuable species are most often cited as belonging to three genera: *Citrullus* (watermelon), *Cucumis* (cucumber and muskmelon) and *Cucurbita* (pumpkins, squash and gourds). However, based on economic importance, an additional four genera (*Benincasa*, *Lagenaria*, *Luffa* and *Momordica*) contain "major crops" cultivated globally for their fruits; these will be introduced below (Sections 2.1 to 2.4) in order of economic importance. A number of other species (n = 21) are cultivated regionally and are of more local commercial importance (Chomicki et al. 2020); several

of these "minor crops" are also discussed (Section 2.5) to give an idea of their diversity and uses. While we recognize the importance of these minor crops, we had to limit the scope of this strategy to a feasible number of crop species; those not explored in detail here merit further study and should be the focus of future crop conservation strategies. Further details of the economic importance of each crop are provided in a supplemental study (Appendix VII).

2.1 *Cucumis sativus* (cucumber)

Among the cultivated species of the Cucurbitaceae, cucumber (*Cucumis sativus*) is the most economically valuable, with a gross production value of US$40.2 billion in 2016 (including gherkins). The production value of cucumber has increased dramatically over time, with a near tenfold increase from US$4.6 billion in 1991 to today (FAOSTAT 2018). Among the 24 vegetable crops recognized by the FAO, cucumbers and gherkins currently rank third in terms of total production (6.9%), following tomatoes (16.7%) and dry onions (8.9%). Global production was 75.2 million metric tonnes in 2018, harvested from a total area of 1.98 million ha across 135 countries. Accounting for 75% of global production, China is by far the largest producer of cucumbers, followed by Iran (3.0%), Turkey (2.5%), Russia (2.1%) and Mexico (1.4%) (FAOSTAT 2018). Cucumber yields average 37.9 tonnes per hectare globally, but vary enormously among nations, from less than one tonne per hectare in Cameroon to 728 tonnes per hectare in the Netherlands. The highest cucumber yields tend to be found

in northern European countries, such as Belgium, Denmark, Finland, Iceland, Ireland, the Netherlands and the UK (FAOSTAT 2018).

Cucumis sativus is a diploid (2n = 14), annual creeping vine with unbranched tendrils that is usually monoecious, though newer cultivars tend to be gynoecious (Schaffer and Paris 2016). Originating in India (Qi et al. 2013), where populations of the wild progenitor (*Cucumis sativus* var. *hardwickii*) still exist, cultivated *C. sativus* is now widespread, growing in both temperate and tropical climates. Cucumber fruits may vary in color (green, white, yellow or orange), size (lengths from 10 cm to 50 cm or more), shape and spine characteristics (Vora et al. 2014). Some authors have categorized cultivars into six main groups using fruit characteristics and geographic origins: French cornichons, European greenhouse cucumbers, American pickling cucumbers, American slicing cucumbers, Middle Eastern cucumbers and Far Eastern cucumbers (Schaffer and Paris 2016). The shorter types are most commonly used for pickling, while longer varieties are eaten raw or cooked. Largely composed of water (often over 90%), cucumbers are also rich in nutrients, such as antioxidants (e.g., beta-carotene, manganese, vitamin C and a number of flavonoids) and trace minerals (e.g., magnesium, potassium, silica and sulfur). Cucumbers have also been used traditionally for therapeutic benefits, such as to combat skin inflammation, to rehydrate and to calm the digestive system (Murad and Nyc 2016; Minh 2019).

High, inter-annual yield variability is a common feature of cucumber production, as a result of the crop's sensitivity to changes in the weather and unsuitable cultivation conditions (Kalbarczyk 2010). As a result, yield (and its components, e.g., branching, disease resistance, earliness, fruit size and sex expression) and fruit quality traits have been a major focus of cucumber breeding efforts to date (reviewed in Pitrat 2008). In many parts of the world, low genetic diversity among cultivars (owing to market demand for a uniform product) also presents a risk to cucumber production, by increasing crop vulnerability to novel diseases and pests (Clark et al. 1996). To enhance abiotic stress tolerance and yield, vegetable grafting is commonly employed in cucumbers (Xu et al. 2016); this horticultural technique bonds cucumber seedlings (the "scions") to the root system of another, more resistant plant species (the "rootstock"). For example, grafting cucumbers onto hybrid *Cucurbita* rootstocks enhances growth under conditions of copper toxicity and salt stress (e.g., Rouphael et al. 2008; 2012), while use of *C. ficifolia* rootstocks provides superior cold tolerance (Li et al. 2014); grafting onto *Luffa cylindrica* boosts heat tolerance, while *Momordica charantia* provides nematode resistance (El-Eslamboly and Deabes 2014).

Figure 2.1 *Cucumis sativus*. Source: World Vegetable Center

Figure 2.2 *Citrullus lanatus*. Source: World Vegetable Center

2.2 *Citrullus lanatus* (watermelon)

Sweet or dessert watermelon (*Citrullus lanatus*) is a globally important primary fruit crop that ranks second only to banana in terms of production. Among the 39 primary fruit crops recognized by the FAO, watermelon accounted for 12% of total production and banana 13.3% in 2018 (FAOSTAT 2018). The global market for watermelon has increased over time, and

the gross production value of watermelons currently hovers around US$34 billion. This makes watermelon the second most economically important cultivated species of the Cucurbitaceae, following cucumber. Global production was 103.9 million metric tonnes in 2018, harvested from a total area of 3.2 million ha in 118 countries (FAOSTAT 2018). Accounting for 61% of global production, China is by far the largest producer of watermelons; other important producers include Iran (4.0%), Turkey (3.9%), India (2.4%), Brazil (2.2%) and Algeria (2.0%). Watermelon yields average 32.1 tonnes per hectare globally, but there is substantial variation, and the highest yields tend to be found in countries in regions with long, hot summers (e.g., Greece, Guyana, Jordan, Palestine and Spain).

Citrullus lanatus is a diploid (2n = 22), annual, monoecious climbing or trailing vine with branching tendrils (Schaffer and Paris 2016). Belonging to the xerophytic genus *Citrullus*, *C. lanatus* is adapted to survive in drought-prone environments. Originating in western Africa (Chomicki and Renner 2015), where wild populations naturally occur, watermelon crops require long, hot summers in order to mature their large, non-climacteric fruits (which do not continue to ripen after harvesting) (Kyriacou et al. 2016). Extremely phenotypically diverse, with more than 1,000 cultivated varieties (Perkins-Veazie et al. 2012), watermelon is primarily grown for consumption of its fresh fruit and seeds. Fruits have a hard outer rind (the exocarp and mesocarp) and fleshy center (endocarp) filled with seeds (Cerri and Reale 2020). While most cultivars have red-colored flesh (due to the presence of the carotenoid lycopene; Tarazona-Díaz et al. 2011), some genotypes have orange, pink, white, yellow or even green flesh (Gusmini and Wehner 2005). Fruits also vary in shape and size (from 2 kg to over 100 kg), rind color and pattern, and the flavor and texture of the flesh (Paris 2015). While largely composed of water (~90%), watermelons also contain important nutrients, such as amino acids (e.g., arginine, citrulline and glutathione), antioxidants (e.g., ascorbic acid, beta-carotene, flavonoids and lycopene), potassium and sugars (Perkins-Veazie et al. 2012; some of these phytochemicals have known beneficial health effects (Maoto et al. 2019). Watermelon can be eaten raw or pickled, and is also incorporated into a variety of products (e.g., confectionaries, juices, jams and sauces) (Maoto et al. 2019). The rind, which is high in citrulline and total phenolics, is also edible when cooked and often used as an additive to drinks, juices or other products owing to its potential health benefits (Tarazona-Díaz et al. 2011). Lastly, watermelon seeds are consumed in some parts of the world (e.g., China and India; Yang and Walters 1992), but elsewhere triploid (3n = 33) seedless cultivars are growing in popularity (Wijesinghe et al. 2020).

Despite the phenotypic diversity seen in watermelon cultivars, their genetic diversity is low (Levi et al. 2001), even in comparison to other Cucurbitaceae crops such as melons (Nimmakayala et al. 2014). The high genetic similarity among cultivars makes them especially vulnerable to pests and disease, and watermelon yields also depend heavily on adequate soil fertility and quality (e.g., Eifediyi et al. 2017). Recent breeding efforts have focused on addressing these challenges, improving fruit quality and introducing new diversity into the cultivated watermelon gene pool (Zhang et al. 2012a; Kyriacou et al. 2018). As with cucumber, vegetable grafting is commonly used to address yield losses in watermelon due to soilborne pathogens and abiotic stresses, such as soil heavy metal contamination, nutrient deficiencies and salinity (Kyriacou et al. 2018). *Cucurbita* interspecific hybrids (e.g., *C. maxima* × *C. moschata*) are popular rootstocks, but may negatively affect fruit quality (Pico et al. 2017). To this end, there may be promise in using other *Citrullus* species as rootstocks (e.g., citron melon, *C. lanatus* var. *citroides*; or bitter apple, *C. colocynthis*) as fruit quality may be less adversely affected (Bigdelo et al. 2017; Fredes et al. 2017).

2.3 *Cucumis melo* (muskmelon)

Muskmelon (*Cucumis melo*) is among the most economically important fruit crops, ranking 11th among the 39 primary fruit crops recognized by the FAO and accounting for 3.2% of total production (FAOSTAT 2018). The global market for melons has increased over time to a current gross production value of roughly US$13.2 billion (up from US$4.2 billion in 1991), a bit over a third of the value of watermelon. Global production was 27.3 million metric tonnes in 2018, harvested from a total area of 1.05 million hectares in 95 countries, with an average yield of 26.1 tonnes per hectare (FAOSTAT 2018). The majority of melon production occurs in Asia (73%), with China the individual nation accounting for the greatest share of production (47%), followed by Turkey (6.4%), Iran (6.3%) and India (4.5%).

Figure 2.3 *Cucumis melo*. Source: Renee Comet/Wikimedia

Cucumis melo is a diploid (2n = 24), annual trailing vine with unbranched tendrils that is commonly andromonoecious or monoecious (Schaffer and Paris 2016). Modern muskmelon cultivars originated in the Near East and parts of Central Asia (Sebastian et al. 2010; Endl et al. 2018), and as such prefer a hot, dry climate; excessive humidity may lower fruit quality. Domestication of muskmelons originally focused on its nutritional seeds, with selection for fruit size only occurring later in the process (Blanca et al. 2012). Since then, muskmelons have highly diversified, particularly in terms of fruit phenotypes, which can vary in shape, size, color and taste/texture (Stepansky et al. 1999). Up to 19 botanical subgroups have been identified in an attempt to classify cultivar diversity (e.g., Robinson and Decker-Walters 1997; Pitrat 2008; Pitrat 2017; Yano et al. 2020), though the details remain contentious (Blanca et al. 2012), and all groups are easily hybridized (Schaffer and Paris 2016). Well-known cultivars include orange-fleshed cantaloupes (with a netted rind), Persian melons (lightly netted rind) and green-fleshed honeydews (smooth-skinned). Interestingly, *C. melo* includes both climacteric (i.e., produce ethylene and continue to ripen after harvest) and non-climacteric fruit types, a fact that has led to considerable research attention focused on ethylene production (Pech et al. 2008). While not an important source of dietary calories, melons are high in fiber, sugar and nutrients such as ascorbic acid (vitamin C), beta-carotene (provitamin A, in the orange-fleshed varieties) and potassium (Lester 1997). For example, daily vitamin C requirements can be met with one-quarter of a cantaloupe (Munger et al. 1995). Melons are typically eaten raw, though immature fruits may be cooked or pickled, and the phytochemicals they contain can have health benefits (Laur and Tian 2011).

Melons are particularly susceptible to fungal, soil-borne pathogens, and these are seen as an increasing problem as a result of continuous cropping practices (Ambrósio et al. 2015). Important pathogens include *Didymella bryoniae* (gummy stem blight), *Fusarium oxysporum* f. sp. *melonis* (Fusarium wilt) and *Fusarium solani* (crown and foot rot), *Monosporascus* spp. (root rot and vine decline disease), *Macrophomina phaseolina* (charcoal rot), and *Sclerotinia sclerotiorum* (Verzera et al. 2014; Castro et al. 2020). As with cucumber and watermelon, vegetable grafting is also commonly employed in melons to enhance abiotic and biotic stress resistance. Grafting commonly occurs onto *Cucurbita* species and interspecific hybrids, as well as white gourd (*Benincasa hispida*), but may detrimentally affect fruit quality. For this reason, the use of rootstocks belonging to the same species or genus (e.g.*, Cucumis metuliferus*) is under investigation, with the added benefit of greater resistance to nematodes (Cáceres et al. 2017; Expósito et al. 2018).

2.4 Pumpkins, squash and gourds

FAO groups pumpkins, squash and gourds together into a single commodity, as none has sufficient international prominence on its own. This group includes a large number of cultivated Cucurbitaceae species, representing both major and minor crops. Major crops in alphabetical order include: *Benincasa hispida, Cucurbita argyrosperma*, *Cucurbita maxima*, *Cucurbita moschata*, *Cucurbita pepo*, *Lagenaria siceraria*, *Luffa acutangula, Luffa cylindrica* and *Momordica charantia*. These are discussed below. Minor crops, reviewed in Section 2.5, include: *Coccinia grandis*, *Cucurbita ficifolia*, *Momordica balsamina*, *Momordica cochinchinensis*, *Momordica dioica*, *Trichosanthes cucumerina* and *Trichosanthes dioica*.

Collectively, pumpkins, squash and gourds represent an economically valuable group, ranking 10th among the 25 vegetable crops recognized by the FAO and accounting for 2.5% of total production (FAOSTAT 2018). The global market for these crops has increased over time to a current gross production value of US$8.5 billion (up from US$2 billion in 1991), roughly a fifth of the value of cucumber. Global production was 27.6 million metric tonnes in 2018, harvested from an area of 2.04 million ha in 115 countries (FAOSTAT 2018). The largest producer is China (29.6%), followed by India (20.1%), Ukraine (4.8%) and Russia (4.3%). Yields averaged 13.5 tonnes per hectare globally, but this varied among regions: Europe (24.7 t/ha), Oceania (16.4 t/ha), the Americas (16.1 t/ha), Asia (13.1) and Africa (7.9 t/ha).

There are four major cultivated *Cucurbita* species (in alphabetical order): *C. argyrosperma*, *C. maxima*, *C. moschata* and *C. pepo*. All are diploid (2n = 40), annual and monoecious, and most take the form of herbaceous vines with branched tendrils (Schaffer and Paris 2016), although non-vining cultivars have been developed for *C. maxima* and *C. pepo*. The genus is native to the Americas (Sanjur et al. 2002) and archaeological data have revealed early origins for *Cucurbita* crops, with domestication occurring at least 8,000 years ago, if not earlier for some crops (Ferriol and Picó 2008). In fact, in Native American culture, corn (*Zea mays*), beans (*Phaseolus vulgaris*) and squash (*Cucurbita* spp.) represented the three pillars (or "sisters") of traditional agriculture (OECD 2016). Today, cultivated *Cucurbita* species are highly diverse and grown worldwide for their edible seeds and fruits, which may be harvested immature or at maturity, depending on the species. Seeds are important sources of oils (especially non-saturated fatty acids) and proteins, while fruits contain carbohydrates and vitamins. Rich in phytochemicals (e.g., carotenoids such as beta-carotene, phenolic compounds and tocopherols),

Cucurbita species have also long been used in traditional medicine to treat gastrointestinal diseases and internal parasites (Salehi et al. 2019). Flowers and certain vegetative parts may also be consumed (Nee 1990), and inedible fruits are used for ornamental purposes or as containers. Cultivated *Cucurbita* species are also commonly used for animal fodder (OECD 2016).

Other major Cucurbitaceae crops (in alphabetical order) include five species of gourd: *Benincasa hispida* (2n = 24), *Lagenaria siceraria* (2n = 22), *Luffa acutangula* (2n = 26)*, Luffa cylindrica* (2n = 26) and *Momordica charantia* (2n = 22). These species are disparate in terms of origins, with *B. hispida* and *L. cylindrica* originating in Southeast Asia (Schaefer et al. 2009), *L. acutangula* in the Arabian Peninsula/India (Filipowicz et al. 2014), and *L. siceraria* and *M. charantia* in Africa (though *L. siceraria* was independently domesticated in Eurasia and South America) (Schaefer and Renner 2010; Kistler et al. 2014). However, all are annual, monoecious vines, grown for their edible fruits (Schaffer and Paris 2016) that are particularly important to smallholder farmers, especially in Southeast Asia (Dhillon et al. 2017), where they represent an important source of calcium, iron and vitamins A and C (Pandit and Acharya 2008). *Luffa* fruits are also prized when mature for their structural properties, forming natural sponges or "loofahs."

2.4.1 *Benincasa hispida* (wax gourd)

The wax gourd (*Benincasa hispida*), alternatively known as ash gourd, Chinese squash, white gourd, white pumpkin and winter melon, is an important warm-season regional crop in Southeast Asia (Schaffer and Paris 2016; Dhillon et al. 2017). Mature fruits are green with a characteristic waxy cuticle, but may vary in shape and size. Some authors have grouped cultivars on the basis of various phenotypic traits (e.g., Walters and Decker-Walters 1989; Bates and Robinson 1995; Marr et al. 2007), with at least four major groups: unridged winter melons, ridged winter melons, fuzzy gourds (covered in hairs rather than waxy) and wax gourds. Many landraces also remain popular in different parts of Asia, and the crop remains relatively underdeveloped commercially (Resmi 2004). Fruits may be consumed immature (usually cooked or pickled) or mature (used in soups), and can also be used in confectionary (Pessarakli 2016). Apart from its nutritional value, wax gourd has also long been valued in Ayurvedic medicine. Current breeding efforts in wax gourd are focused on assessing available genetic diversity and the potential for heterosis (also known as hybrid vigor) (Verma et al. 2007).

Figure 2.4 *Benincasa hispida.* Source: Ingridinsydney/Wikimedia

Figure 2.5 *Cucurbita argyrosperma*. Source: Fernando Lopez Anido/Wikimedia

2.4.2 *Cucurbita argyrosperma* (cushaw, silver-seeded gourd)

The cushaw (*Cucurbita argyrosperma*), or silver-seeded gourd, is a mesophytic native of the lowlands of Mexico (Schaffer and Paris 2016), where it interbreeds naturally with sympatric wild relatives (Nee 1990). Today, cultivated forms are found from Mexico

through Central and South America, where the cushaw is an important subsistence crop (Sánchez-de La Vega et al. 2018). Cushaw is mainly cultivated for its edible seeds (high in oil and protein) or grown as forage, because the fruit flesh is generally low in quality (Lira-Saade 1995); however, several improved cultivars, grown for their fruit flesh, exist in the USA (e.g., 'Green Striped Cushaw,' 'Hopi,' 'Magdalena Striped,' 'Veracruz Pepita' and 'White Cushaw') (OECD 2016). Nonetheless, most contemporary cultivation remains based on landraces and local varieties (OECD 2016). *Cucurbita argyrosperma* is also considered less phenotypically diverse than other species of *Cucurbita* (Ferriol and Picó 2008). Genetic diversity studies of domesticated *C. argyrosperma* subsp. *argyrosperma* have revealed patterns of isolation-by-distance within Mexico, identified the highest levels of diversity in southern Mexico and provided evidence for ongoing geneflow with the wild progenitor, *C. argyrosperma* subsp. *sororia* (Montes-Hernandez and Eguiarte 2002; Sánchez-de La Vega et al. 2018).

2.4.3 *Cucurbita maxima* (pumpkin, winter squash)

Cultivated *Cucurbita maxima* is native to warm-temperate regions of South America, where it was domesticated before dissemination to Eurasia and Africa during the Columbian exchange (OECD 2016; Kates et al. 2017). Today, *C. maxima* (variously known as Hubbard squash, kabocha squash, pumpkin, winter squash, among other names, depending on the variety) is one of the most widely grown *Cucurbita* crops; it is cultivated worldwide, with a secondary center of diversity in Asia (Ferriol et al. 2004). It is also considered the second most phenotypically diverse, following *C. pepo* (Ferriol and Picó 2008), with a broad diversity of fruit characteristics, including coloration patterns, shapes and sizes. To classify this diversity, horticultural groups were proposed for *C. maxima* as early as the 20th century (Castetter 1925; Whitaker and Davis 1962, Decker-Walters and Walters 2000), often recognizing six groups: "Banana" (long, pointy fruits), "Delicious," (turbinate-shaped, with high-quality flesh), "Hubbard" (oval fruits with pointed or curved ends and a hard rind), "Marrow" (soft-skinned and lemon-shaped), "Show" (very large and globular, orange-colored fruits) and "Turban" (turban-shaped with a hard rind). Certain "Show" type cultivars produce massive pumpkins that weigh in the hundreds of kilograms (e.g., 'Mammoth Chilli' and 'Mammoth Whale') used for shows and competitions (OECD 2016). More recently, "Kabocha" type cultivars have been developed in Japan; most are F_1 hybrids developed from open-pollinated *C. maxima* varieties (Ferriol and Picó 2008). Kabocha squash is prized for its culinary properties and its sweet, nutty flavor (Morgan and Midmore 2003). While immature *C. maxima* fruits are

Figure 2.6 *Cucurbita maxima.* Source: George Chernilevsky/ Wikimedia

consumed in South America, elsewhere the consumption of mature fruits is more common, or the fruits are used for ornamental purposes (Schaffer and Paris 2016).

Among the *Cucurbita* species, *C. maxima* is the most tolerant of low temperatures, and some varieties also possess resistance to viral diseases (OECD 2016). Additionally, *C. maxima* has often been used to facilitate interspecific crosses within the genus (Ferriol and Picó 2008) and to produce new commercial hybrids with beneficial agronomic traits, especially with *C. moschata* (Murkovic et al. 2002). Hybrid rootstocks, in particular *C. maxima* × *C. moschata*, are also widely used for the grafting of other cucurbit species (e.g., cucumber, melon and watermelon) (Pico et al. 2017). Praised for their versatility, these hybrid rootstocks may enhance cold and heat tolerance, increase nutrient and water use efficiency, and also provide disease resistance to soilborne pathogens (Lee et al. 2010; Pico et al. 2017 and references therein).

2.4.4 *Cucurbita moschata* (butternut squash, tropical pumpkin)

The exact origins of butternut squash (*Cucurbita moschata*) remain a mystery, but domestication likely occurred somewhere in the tropics of South America (Sanjur et al. 2002), where the greatest diversity of landraces currently exists (Chomicki et al. 2020). Today, butternut squash is cultivated in tropical and subtropical regions worldwide for the consumption of its high-quality, mature fruits; especially in parts of the Caribbean, Central and South America, butternut squash represents an important source of

Figure 2.7 *Cucurbita moschata.* Source: George Chernilevsky/ Wikimedia

Figure 2.8 *Cucurbita pepo.* Tim Sackton/Wikimedia

nutrients (e.g., fiber, magnesium, potassium, provitamin A and vitamin C) in the diet (Schaffer and Paris 2016; Salehi et al. 2019). The crop may also be used as animal fodder, and is widely appreciated in traditional medicine (Pessarakli 2016). For example, toasted seeds are eaten to treat intestinal parasites, while the fruits have anti-inflammatory properties and their consumption may alleviate digestive ailments (Govindani et al. 2012). As with other *Cucurbita* species, *C. moschata* fruits are highly diverse (in color, durability, rind hardness, shape, size, etc.) (OECD 2016), and commercial cultivars are commonly grouped into three horticultural types: "Butternut-Bell" (flared to almost cylindrical in shape), "Cheese" (oblong, buff-colored fruits) and "Crooknecks" (rounded fruit with a long neck). However, these commercial types fail to capture the global diversity of tropical landraces (Ferriol and Picó 2008), which are adapted to a broad range of agro-ecological conditions and vary in important agronomic traits (disease resistance, flowering habits, leaf characteristics, etc., as well as fruit type) (Du et al. 2011).

Within the genus, *C. moschata* has the best crossability with congeneric cultivated species (OECD 2016). It also serves as an important reservoir of resistance to pathogens, such as cucumber mosaic virus (CMV), Fusarium wilt, papaya ringspot virus (PRSV), tomato leaf curl New Delhi virus (ToLCNDV), watermelon mosaic virus (WMV) and zucchini yellow mosaic virus (ZYMV) (Traka-Mavrona et al. 2000; Brown et al. 2003; Sáez et al. 2020). These resistance traits may be transferred to susceptible species (e.g., *C. pepo*) via interspecific crosses (OECD 2016). *Cucurbita moschata* may also be used as a rootstock in grafting other *Cucurbita* species (e.g., cucumber, melon and watermelon) (Pico et al. 2017). Hybrid rootstocks of *C. maxima* × *C. moschata* are most commonly used, but single-species *C. moschata* rootstocks have had some success

(e.g., in grafting cucumber, Liu et al. 2012); grafting provides protection from a variety of soilborne diseases and alleviates the effects of abiotic stresses (Lee et al. 2010).

2.4.5 *Cucurbita pepo* (summer squash, zucchini)

Cucurbita pepo is the most widely grown *Cucurbita* species, originally domesticated in Mexico, but now cultivated in temperate zones worldwide (Chomicki et al. 2020). As a crop, *C. pepo* is extremely diverse, with multiple subspecies and varieties, and a plethora of cultivars, varying tremendously in fruit morphology (Paris 2008). Depending on the variety, *C. pepo* may be grown for its edible immature or mature fruits, seeds (or seed oil) or as an ornament (Schaffer and Paris 2016). The immature fruits, known as summer squash, vary in color (diverse shades of green, yellow or orange), patterning (uniform or variegated), rind features (lignified or non-lignified, and smooth, warted, wrinkled, etc.), shape (round to cylindrical to flat-scalloped) and size (less than 100 g to over 20 kg when mature) (OECD 2016). Summer squash cultivars are classified into six groups based on fruit shape: "Cocozelle," "Crookneck," "Scallop," "Straightneck," "Vegetable Marrow" and "Zucchini" (see Paris 2008 for illustrations). "Zucchini" types are the most commonly cultivated group. Varieties of *C. pepo* grown for their mature fruits are classified into two cultivar groups: "Acorn" (including a number of winter squashes) and "Pumpkin" (includes edible types, such as pie pumpkins, or those used for ornamental purposes). Lastly, there are three cultivar groups grown exclusively for ornamental purposes: "Oviform, Smooth-Rinded Gourd," "Round, Smooth-Rinded Gourd" and "Warted Gourd;" these produce bitter, small fruits that have colorful, hard rinds. The edible fruits and seeds of *C. pepo* also have a long history in folk medicine where they are used in treatments for

Figure 2.9 *Lagenaria siceraria*. Source: World Vegetable Center

Figure 2.10 *Luffa acutangula*. Source: World Vegetable Center

intestinal parasites and other gastrointestinal problems (Younis et al. 2000; Salehi et al. 2019).

Breeding efforts in *C. pepo* are often region-specific, as consumer preferences for fruit type vary among regions (Paris 2008), yet traits such as earliness and high productivity are universally desirable. New and improved summer squash cultivars have largely replaced traditional landraces over the last century (Formisano et al. 2012), and, owing to high levels of heterosis, many successful cultivars are F_1 hybrids, which have greater productivity and vigor (Paris 2008). A gene responsible for the non-vining bush phenotype in *C. pepo*, useful in high-density plantings, has also been transferred to two other cultivated species (*C. argyrosperma* and *C. moschata*) (OECD 2016). Disease resistance in *C. pepo* remains a challenge, as there is a lack of resistance genes in *C. pepo*, necessitating costly and difficult work with interspecific hybrids (to transfer resistance genes from other *Cucurbita* species) (Paris 2016). In particular, summer squash still lacks truly virus-resistant cultivars, such as those seen for cucumber. The use of genetic engineering technologies may be useful in this regard (Gaba et al. 2004).

2.4.6 *Lagenaria siceraria* (bottle gourd)

The bottle gourd (*Lagenaria siceraria*), also known as calabash or white-flowered gourd, has been domesticated multiple times in different regions of the globe, for a variety of purposes (Schaffer and Paris 2016). This independent selection has produced a tremendous diversity of fruit types, shapes and sizes (see Dhillon et al. 2017 for examples). Younger fruits may be consumed, as well as shoots and tendrils, and the oil may be extracted from seeds (Achigan-Dako et al. 2008b). When eaten, bottle gourds provide carbohydrates, fiber, minerals and vitamins (Pessarakli 2016), and also play a part in traditional Ayurvedic medicine,

for alleviating digestive complaints. However, mature bottle gourds have been most highly prized for other uses, particularly as various types of containers (e.g., barrels, cups, ladles and pails) and for crafts (e.g., carvings, jewelry, musical instruments and toys) (Heiser 1979). Upon maturation, the flesh of the bottle gourd dries out, ultimately leaving a hard, dry shell behind. Initial studies of genetic diversity in bottle gourd germplasm collections have revealed strong geographic structure, with Indian accessions being particularly unique (e.g., Levi et al. 2009; Gürcan et al. 2015). Little work has been done to characterize and evaluate accessions, but certain cultivars are gaining popularity as rootstocks for grafting other Cucurbitaceae species; in this regard, bottle gourd rootstocks show resistance to cucurbit powdery mildew (Kousik et al. 2008), downy mildew (Singh 2013), Fusarium wilt (Oda 2002) and various plant viruses (Ling et al. 2013), among other diseases.

2.4.7 *Luffa acutangula* (angled loofah) and *Luffa cylindrica* (smooth loofah)

Angled loofah (*Luffa acutangula*), also known as Chinese okra or ridged gourd, and smooth loofah (*Luffa cylindrica*, synonym *L. aegyptiaca*), also known as sponge gourd, are two annual, monoecious vines (2n = 26) (Marr et al. 2005; Alam et al. 2018), cultivated for their immature and mature fruits (Schaffer and Paris 2016). Both economically important species, these two *Luffa* species have different geographic origins: *L. acutangula* in the Arabian Peninsula and India, and *L. cylindrica* in Southeast Asia (Filipowicz et al. 2014). Today, *Luffa* is cultivated in tropical regions worldwide, including in Central America, China, India, Korea and Japan (Dhillon et al. 2017). In many parts of South, East and Southeast Asia, the immature, cylindrical, green fruits (ridged in the case of angled loofah) are consumed as cooked vegeta-

Figure 2.11 *Momordica charantia*. Source: World Vegetable Center

Figure 2.12 *Cocciniia grandis*. Source: World Vegetable Center

bles, while extracts from many parts of the plants are used in traditional medicine (Marr et al. 2005; Azeez et al. 2013; Pessarakli 2016); the seeds are also eaten roasted. Loofah fruits are more widely appreciated when mature for their structural properties; when dry, the mesocarp forms a fibrous net useful as a sponge (Schaffer and Paris 2016). The dried fruit fibers are used in the production of a variety of products, from bath mats, to engine filters, to insulation (Filipowicz et al. 2014), as well as in gloves, hats and sandals (Pessarakli 2016). For a list of high-yielding, popular cultivars for both species, see Dhillon et al. (2017). Breeding lines are being developed by WorldVeg in collaboration with consortia of breeding consortia and with a focus on ToLCNDV and downy mildew (Dhillon et al. 2020).

2.4.8 *Momordica charantia* (bitter gourd, bitter melon)

Bitter gourd (*Momordica charantia*), also known as African cucumber, balsam pear, bitter cucumber and bitter melon, is a crop of regional importance in South Asia and West Africa (Schaffer and Paris 2016). Bitter in flavor when mature (owing to the presence of momordicine and triterpene glycosides), the green, spindle-shaped bitter gourd fruits are only consumed when immature (Behera et al. 2010), although bitterness has been selectively retained during domestication (as a desirable trait; Marr et al. 2004). Nonetheless, bitter gourds are typically used only in small quantities in combination with other vegetables, and are commonly blanched, parboiled or soaked in saltwater before use to reduce the bitterness (Behera et al. 2010). Flowers and young shoots are also consumed, but the seeds must be avoided as they are poisonous (Schaffer and Paris 2016). Bitter gourd is prized both for its nutritional value (rich in beta-carotene, folic acid, vitamin C and several trace minerals) and for its health benefits in folk medicine, where it has

Figure 2.13 *Cucurbita ficifolia.* Source: F. and I. Salliet/Wikimedia

been used for centuries (Achigan-Dako et al. 2008a). It is particularly valued for its ability to lower blood sugar, and plays a role in managing type 2 diabetes in parts of Asia (Dhillon et al. 2017). Market demands for specific cultivars or landraces of bitter gourd tend to be country-specific (maintaining a broad genetic diversity), but the use of a small number of gynoecious inbred lines in breeding efforts has led to reductions in diversity in commercial cultivars (Dhillon et al. 2017). Commercial breeding has resulted in increases in total and early fruit yield (Dey et al. 2010), but the narrow genetic base puts crops at risk of novel diseases, such as cucurbit aphid-borne yellow virus (CABYV) (Relevante et al. 2012). In response to this threat, WorldVeg has established a regional breeding program with a consortium of companies to broaden the genetic basis of commercial varieties of bitter gourd in South and Southeast Asia (Dhillon et al. 2016; Dhillon et al. 2020). This program aims to broaden the genetic basis for bitter gourd breeding in this region and to develop varieties that are resistant to cucurbit powdery mildew (caused by *Podosphaera xanthii*).

2.5 Minor crops

2.5.1 *Coccinia grandis* (ivy gourd)

Ivy gourd (*Coccinia grandis*), also known as scarlet gourd, is a perennial, dioecious vine (2n = 24), that is relatively unique among plants, as it has heteromorphic sex chromosomes (Ming et al. 2011). Originating in East Africa, it is now a crop of regional importance in tropical parts of Southeast Asia (Chomicki et al. 2020), an in India, where it has been used for centuries in traditional medicine (Nagare et al. 2015). For example, leaf extracts may have analgesic properties, and have long been used to treat inflammatory conditions such as rheumatism (Hossain et al. 2014). The bitter, red fruits (technically many-seeded berries, or "pepos") are consumed as a vegetable (both ripe and unripe), as are the leaves and young shoots; both are high in carotenoids (e.g., beta-carotene and lycopene), which makes ivy gourd especially important as a source of vitamin A in developing countries (Holstein 2015). Currently an underutilized crop, *C. grandis* is only partially domesticated to date and has not been the focus of much breeding effort, though some promising cultivars exist in South Asia (Bharathi 2007). In some parts of the world, *C. grandis* is regarded as a weed because of its rapid growth; for example, it is listed as an invasive species on Pacific Islands such as Hawaii (Hawaiian Ecosystems at Risk Project 2013), where it is naturalized.

2.5.2 *Cucurbita ficifolia* (fig-leaf gourd)

Fig-leaf gourd (*Cucurbita ficifolia*) is so named based on the deeply lobed shape of its leaves, which resemble those of fig plants (Grubben 2004). A monoecious climbing vine, which possesses the characteristic tendrils of the *Cucurbita*, *C. ficifolia* (2n = 40) is an annual when grown in temperate climates, but may grow as a short-lived perennial in the tropics (OECD 2016). Widely grown throughout the Americas, the fig-leaf gourd is a cold-tolerant species well adapted to cultivation at higher altitudes (Schaffer and Paris 2016). Certain landraces are also grown in other parts of the world (e.g., Europe, India and Japan), but *C. ficifolia* has a narrower distribution than other cultivated *Cucurbita* species, in part due to its short-day requirement for flowering (Ferriol and Picó 2008). In contrast to the high variability known in other *Cucurbita* species, fig-leaf gourd is also low in genetic and morphological diversity (Andres 1990; Ferriol et al. 2005). The fruits are fairly uniform, round to oblong in shape (resembling a watermelon), weighing several kilograms, and usually mottled green and white in color (Schaffer and Paris 2016), with broad black seeds (Nee 1990). Most often grown for consumption of their white, fibrous fruit flesh, fig-leaf gourds are eaten raw, candied or used in making beverages and

Figure 2.14 *Momordica cochinchinensis*. Source: World Vegetable Center

preserves (OECD 2016); seeds may also be consumed toasted, as done by Andean communities among whom this crop is known as sambo squash (Skarbø 2016). There are only a few *C. ficifolia* commercial cultivars, which are commonly used as rootstocks for grafting other species, such as cucumber (Pavlou et al. 2002; Pico et al. 2017). *Cucurbita ficifolia* is naturally tolerant to abiotic stresses such as cold and salinity, and may serve as a reservoir of resistance genes for cucurbit breeding (Lee and Chung 2005; Wang et al. 2006).

2.5.3 *Momordica balsamina* (balsam apple), *Momordica cochinchinensis* (gac) and *Momordica dioica* (spiny gourd)

In addition to bitter gourd (*Momordica charantia*), three other minor crops exist in the genus: balsam apple (*M. balsamina*, also known as African pumpkin), gac fruit (*M. cochinchinensis*) and spiny gourd (*M. dioica*) (Chomicki et al. 2020). All three minor crops are tropical climbing vines, bearing spiny fruits containing large, inedible seeds surrounded by red arils and colorful fruit flesh/pulp (Behera et al. 2010; Nagarani et al. 2014). *Momordica balsamina* is a monoecious annual (2n = 22) with bright red fruits, and is closely related to *M. charantia* (Hassan and Umar 2006; Schaefer and Renner 2010; Bharathi et al. 2011); *M. cochinchinensis* and *M. dioica* are dioecious perennials (2n = 28) and have orange-red and green fruits, respectively (Talukdar and Hossain 2014; Chuyen et al. 2015). In terms of geographic origins, the natural distribution of *M. balsamina* extends throughout Africa and West Asia, while that of *M. cochinchinensis* ranges from Southeast Asia to northern Australia, and that of *M. dioica* falls within South Asia (Chomicki et al. 2020). Fruits are typically harvested from wild populations, but all three species are also cultivated in various parts of their ranges; however, only *M. cochinchinensis*

shows evidence of domestication, in the form of larger fruits (600 g or more; Behera et al. 2010; Chomicki et al. 2020).

Momordica balsamina is valued for both its nutritional and medicinal properties (Thakur et al. 2009). The leaves and arils (i.e., seed coverings) are edible, but the flesh and seeds of mature fruits are likely poisonous (Diaz 2016). In particular, the leaves are relatively high in amino acids and minerals (e.g., Ca, Cu, Fe, K, Mg and Mn), and may be useful as a protein supplement in rural communities, where diets are largely cereal-based (Hassan and Umar 2006). Leaf and fruit extracts are traditionally used as antiseptics (Diaz 2016), and may also have useful antiviral properties (Bot et al. 2007; Kaur et al. 2013). Similarly, all parts of *M. dioica* plants are also used for medicinal purposes (Talukdar and Hossain 2014), while the immature spiny gourd fruits are consumed as a vegetable throughout Southeast Asia (Behera et al. 2010); fruits are rich in protein, and also supply carbohydrates, fiber, iron, lipids and minerals (e.g., Ca and P). Spiny gourds also contain the highest levels of beta-carotene (a precursor of vitamin A) among the cucurbits (Talukdar and Hossain 2014).

Gac (*M. cochinchinensis*) is the best known and most widely cultivated of the three minor *Momordica* crops. As a result of recent interest from the general public and scientific community, many new farming enterprises for gac have been established in subtropical and tropical regions worldwide (Huynh and Nguyen 2019). Immature fruits and leaves are consumed (Behera et al. 2010), and the fruit flesh (mesocarp) and arils are particularly high in beta-carotene and lycopene (Aoki et al. 2002). The red arils have long been used as a natural food colorant (Chuyen et al. 2015), and are produced commercially for food and cosmetic applications (Huynh and Nguyen 2019). Gac plants are a rich source of many bioactive phytochemicals (reviewed by Huynh and Nguyen 2019), used in traditional medicine (Pessarakli 2016), and with high potential for agricultural, industrial and medicinal applications (Osman 2017). Although there has been little in the way of cultivar selection or breeding efforts to date (Behera et al. 2010), preliminary studies from Southeast Asia show high levels of genetic diversity and phenotypic diversity for agronomic traits of interest (e.g., Bootprom et al. 2012; Wimalasiri et al. 2016; Pham et al. 2017; Ho et al. 2019).

2.5.4 *Sechium edule* (chayote)

Chayote (*Sechium edule*) is a monoecious, perennial climbing vine (2n = 24) that is native to Mexico, but now grown in subtropical and tropical regions

Figure 2.15 *Sechium edule.* Source: David Monniaux/Wikimedia

worldwide (Bisognin 2002; Schaffer and Paris 2016). Key producers of chayote fruit include Brazil, Costa Rica, the Dominican Republic and Mexico (Lim 2012). The two largest producers, Mexico and Costa Rica, export a significant percentage of their crop, much of it to Canada and the USA, where there has been a recent surge in demand (Cadena-Iñiguez et al. 2007). While only the mature fruits are exported (and hence important for trade), virtually the whole plant (including the immature fruits, leaves and tuberous roots) is edible and typically consumed or used for fodder (Del Ángel Coronel et al. 2017). The single-seeded mature fruits are highly variable, ranging in their appearance (smooth to deeply ridged or spiny), color (white to dark green), flavor (from bitter to slightly sweet or starchy), shape (pyriform to spherical) and size (Lira-Saade 1996). Local preferences in producing countries dictate the prevalence of a diversity of types (see Cadena-Iñiguez et al. 2007 for examples), which are valued both for their nutritional and pharmaceutical properties (Loizzo et al. 2016). However, only a few types are commercially cultivated and a single type is traded internationally (the smooth, green "*virens levis*" type, which dominates commercial markets) (Vieira et al. 2019). No systematic breeding programs exist for chayote yet, although these are needed to combat pests and diseases, and prolong the longevity of harvested chayote fruits; fruits are highly perishable and especially vulnerable to fungal pathogens (Cadena-Iñiguez et al. 2007). This short shelf life has, however, prompted the development of processed products (e.g., confectionary, jams, sauces and pickles) and dehydrated offerings (Vieira et al. 2019). The shoots of *Sechium edule* are a popular leafy vegetable in Southeast Asia and the Pacific. Known as choko tips, it ranks among the most popular traditional vegetables in Papua New Guinea (Solberg et al. 2018).

2.5.5 *Trichosanthes cucumerina* (snake gourd) and *Trichosanthes dioica* (pointed gourd)

Snake gourd (*Trichosanthes cucumerina*) and pointed gourd (*Trichosanthes dioica*) are two minor subtropical and tropical crops belonging to the largest genus within the Cucurbitaceae family. Both species are vines (2n = 22), but while snake gourd is a monoecious annual with non-tuberous roots, pointed gourd is a dioecious perennial with tuberous roots (Bharathi et al. 2013). Snake gourd, so named for its long, cylindrical, twisted fruits (that resemble snakes), is cultivated in tropical regions worldwide, but commercially cultivated only in China, India, Japan and Sri Lanka (Dhillon et al. 2017). Pointed gourd, which has shorter, oblong fruits, is most extensively cultivated only in Bangladesh, India, Nepal and Sri Lanka (Bharathi et al. 2013). The fruits of both species, typically consumed when immature (before they become bitter), are eaten as cooked vegetables, and the red pulp of mature snake gourds may be used similarly to tomato paste in prepared dishes (Achigan-Dako 2008; Bharathi et al. 2013). A variety of high-yielding cultivars have been developed for both gourd species to date, most based on farmer selections of local land-

Figure 2.16 *Trichosanthes cucumerina*. Source: World Vegetable Center

races; for pointed gourd, which is typically propagated vegetatively (i.e., from stem or root cuttings), many cultivars represent individual clones (Kumar and Singh 2012). In recent decades, India has initiated more systematic breeding programs, resulting in the release of superior hybrid cultivars (Bharathi et al. 2012; Dhillon et al. 2017).

Benincasa hispida (Thunb.) Cogn. as *Benincasa cerifera* Savi. Source: Revue horticole
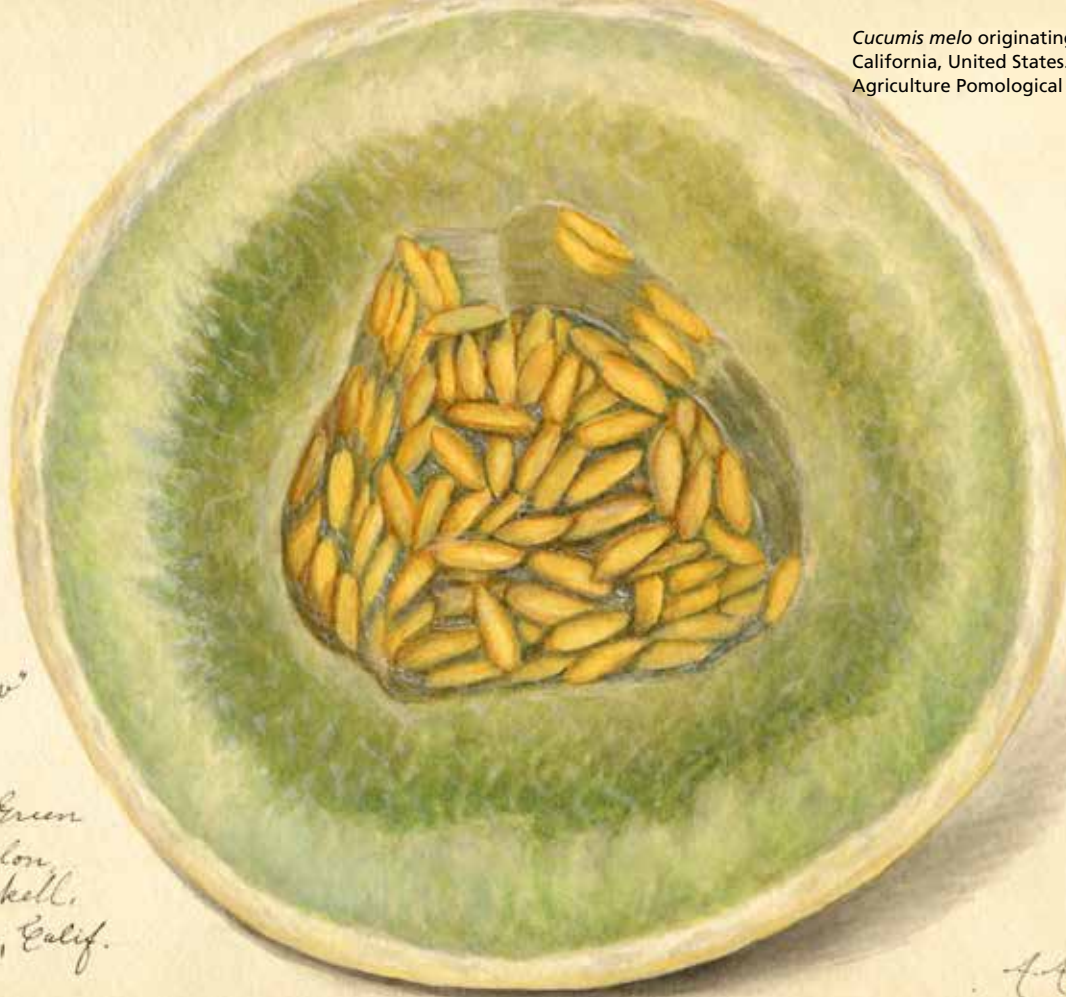
3 TAXONOMY

The Cucurbitaceae family comprises an estimated 95 genera and 965 species, according to a recent review (Christenhusz and Byng 2016) that compiled data from numerous sources. In their review, Christenhusz and Byng (2016) only included accepted and described genera and species, and these numbers may be subject to change following future taxonomic discoveries and revisions; for example, there are many hypothesized Cucurbitaceae species that are not yet fully described. Molecular studies have confirmed the monophyly of the Cucurbitaceae (e.g., Kocyan et al. 2007; Schaefer et al. 2009; Schaefer and Renner 2011), which is closely related to three other families in the order Cucurbitales (the Begoniaceae, Datiscaceae and Tetramelaceae) (Zhang et al. 2006), although the exact phylogenetic relationships among the families remain unclear (Renner and Schaefer 2017). The Cucurbitaceae species are typically subtropical or tropical, annual climbing or trailing vines with lateral tendrils: a distinguishing feature of the family (Schaefer and Renner 2011). Cucurbitaceae species are distributed globally, but about 40% are endemic to the Americas, with many species also occurring in Africa (28%) and Asia (26%) (Lebeda et al. 2007; Schaefer et al. 2009). To date, the most comprehensive phylogenetic analysis of the Cucurbitaceae family is given in Schaefer and Renner (2011), which used molecular data to recognize 15 tribes within the family.

With a long history of association with humans (~12,000 years; Lira-Saade 1995), the Cucurbitaceae is today an economically important family, including some of the world's most important crops, as discussed in Section 2 of this strategy. The following six tribes contain species of major or minor economic importance, as defined by Chomicki et al. (2020): tribe Benincaseae, tribe Cucurbiteae, tribe Joliffieae, tribe Momordiceae, tribe Sicyoeae and tribe Siraitieae (Table 3.1). The taxonomy of the most important cultivated genera is discussed in Sections 3.1 to 3.7.

3.1 *Cucumis*

The genus *Cucumis* L. belongs to the Benincaseae tribe, as described by Schaefer and Renner (2011), and includes more than 60 cultivated and wild species, with 63 accepted species currently listed on GRIN Taxonomy (GRIN-Global 2020). Within the genus, there are two major global crops, cucumber (*C. sativus* L.) and muskmelon (*C. melo* L.), and two wild species

that are also used for commercial fruit production: *C. anguria* L. (West Indian gherkin) and *C. metuliferus* E. Meyer ex Naudin (African horned cucumber or Kiwano) (Chomicki et al. 2020). Although *C. melo* and *C. sativus* were once considered to be closely related, as determined by morphological data (and do occur in the same section with the genus, *Cucumis*), molecular analyses have shown them to be more phylogenetically distant (Chung et al. 2006; Renner et al. 2007). This can be clearly seen in the latest phylogeny for *Cucumis* (Endl et al. 2018), which inferred a maximum likelihood phylogenetic tree based on six plastid and one nuclear locus.

Domesticated cucumbers are descended from a wild form (*C. sativus* var. *hardwickii*) native to India, and may be classified into three genetic groups: a Eurasian group (from West Asia, Europe and the USA), an East Asian group (from China, Korea and Japan) and a Xishuangbanna group (from tropical southwestern China) (Qi et al. 2013). These three groups are monophyletic and each group is relatively genetically homogeneous. The groups may be morphologically distinguished, with Eurasian cucumbers having smooth skins and short stalks, as compared to the relatively longer-stalked, spiny East Asian cucumbers; both the Eurasian and East Asian groups belong to the same variety, *C. sativus* var. *sativus*. Xishuangbanna cucumbers, which are more spherical in shape and have a distinctive orange fruit flesh (the endocarp), belong to a second subspecies, *C. sativus* var. *xishuangbannanensis* (Renner 2017), thought to have originated via diversifying selection post-domestication (Bo et al. 2015). As discussed in Section 2.1, some authors have further categorized Asian and European cultivars into multiple morphological groups.

Muskmelons (*C. melo*) show greater intraspecific complexity than cucumbers, and this diversity has proven

challenging to properly assess and characterize them. Adding to the confusion are repeated taxonomic revisions and changing infraspecific classification schemes. For example, while two subspecies (*agrestis* and *melo*) have long been recognized for muskmelon, based on ovary pubescence (Jeffrey 1980), these have generally not been supported by molecular data, which often show the subspecies to be polyphyletic (see Endl et al. 2018 and references therein, though Zhao et al. 2019 recaptured these two subspecies). By densely sampling both cultivated and wild *C. melo*, as well as most other *Cucumis* species, and then sequencing these at multiple loci, Endl et al. (2018) were able to describe the genetic structure within *C. melo* and shed light on muskmelon's domestication history. Accessions are grouped geographically, forming two distinct lineages: one African (named *C. melo* subsp. *meloides* by the authors) and one Asian/Australian (named *C. melo* subsp. *melo*).

The placement of cultivars within the phylogenetic tree suggested at least two independent domestication events for muskmelon, one in each lineage; this finding has been supported by a more recent study that used a robust single nucleotide polymorphism (SNP) dataset (Zhao et al. 2019). Apart from 'Tibish' and 'Fadasi' cultivated melons (both from Sudan), which belong to the African lineage, all modern melon cultivars belonged to the Asian lineage.

In terms of melon cultivar diversity, patterns of fruit diversity have been described using purely morphological infraspecific classifications, which predate the advent of molecular analyses. For example, the latest such classification recognizes 19 horticultural groups (Pitrat 2017) (Table 3.2), as discussed in Section 2.1. In this classification scheme, the majority of the cultivar groups (except for 'Tibish') belong to the Asian clade (described by Endl et al. (2018)), while the wild group 'Agrestis' likely contains a mix of both lineages. Future

Table 3.1 Six tribes[1] of the Cucurbitaceae family that contain cultivated species.

Tribe[1]	General description	Geographic distribution	Number of genera	Number of species	Major genera
Benincaseae	Dioecious or monoecious, annual or perennial, herbaceous or woody climbers or trailers	Africa, Asia, Australia	24	204–214	*Benincasa, Citrullus, Coccinia, Cucumis, Lagenaria, Melothria*
Cucurbiteae	Monoecious, herbaceous annuals or woody lianas	Southern USA through South America	11	100–110	*Cucurbita, Sicana*
Joliffieae	Dioecious, herbaceous or large woody lianas with tuberous roots	Tropical Africa	3	10	*Telfairia*
Momordiceae	Dioecious or monoecious, herbaceous or woody climbers or trailers	Subtropics and tropics of Africa, Asia & Australia	1	60	*Momordica*
Sicyoeae	Monoecious or dioecious, herbaceous or woody climbers or trailers, with fibrous or woody roots	Pantropical	12	264–266	*Cyclanthera, Hodgsonia, Luffa, Sechium, Trichosanthes*
Siraitieae	Dioecious, herbaceous climbers with enlarged tubers	Southeast Asia	1	3–4	*Siraitia*

[1]Tribes as described by Schaefer and Renner (2011).

infraspecific classification schemes will benefit from ongoing molecular work to describe relationships among cultivar types.

3.2 *Cucurbita*

The genus *Cucurbita* L. belongs to the Cucurbiteae tribe, as described by Schaefer and Renner (2011), and includes 15 accepted cultivated and wild species, as currently listed on GRIN Taxonomy (GRIN-Global 2020). Within the genus, there are five cultivated species, including four major global crops, namely butternut squash (*C. moschata* Duchesne), cushaw (*C. argyrosperma* C. Huber), pumpkin/winter squash (*C. maxima* Duchesne) and summer squash (*C. pepo* L.), as well as one minor crop of regional importance, fig-leaf gourd (*C. ficifolia* Bouché) (Chomicki et al. 2020; Khoury et al. 2020). The *Cucurbita* species may be divided into two ecological groups: mesophytic annuals and xerophytic perennials. The xerophytic perennials are all wild species, characterized by fleshy storage roots, which represent the ancestral state for *Cucurbita* (Kates et al. 2017). The mesophytic annuals include all the cultivated species, as well as a number of wild species, and possess fibrous roots (Lebeda et al. 2007). The latest phylogeny for the *Cucurbita* (Kates et al. 2017) shows the evolutionary relationships among species, as determined using a maximum likelihood approach based on sequence data for 44 nuclear loci.

The cushaw (*C. argyrosperma*) encompasses two subspecies: subsp. *argyrosperma* represents the cultivated form, while subsp. *sororia* represents the wild form of the species (Merrick and Bates 1989; Merrick 1995). However, while recent molecular analyses have supported this progenitor–domesticate relationship (e.g., Sanjur et al. 2002; Zheng et al. 2013), the two subspecies were intermeshed in the genetic structure analysis of Kates et al. (2017), tending to form multiple clusters of mixed cultivated and wild accessions. This pattern is likely indicative of multiple domestication events, a broad domestication bottleneck and/or ongoing crop-wild introgression. For subspecies *argyrosperma*, a recent infraspecific classification groups cultivars into three botanical varieties (Paris 2017): Callicarpa, Silver-seed and Stenosperma.

Similarly, two subspecies are recognized for pumpkins and winter squash (*C. maxima*): a wild form, subsp. *andreana*, and a cultivated form, subsp. *maxima* (Decker-Walters and Walters 2000). However, in contrast to the case with cushaw, a single domestication event was supported for *C. maxima* based on the molecular data (Sanjur et al. 2002; Kates et al. 2017). Various infraspecific classification schemes have been proposed for *C. maxima*, for example the six cultivar group scheme discussed in Section 2.4.3, which includes Banana, Delicious, Hubbard, Marrow, Show and Turban types. Another potential scheme

Table 3.2 Infraspecific classification for cultivated muskmelon (*Cucumis melo*), including the horticultural groups and subgroups delineated by Pitrat (2017).

Group	Subgroups	Cultivation status	Distribution
Agrestis		Wild	Africa, Asia, Australia
Kachri		Intermediate between wild melons & local cultivated types	Africa, Asia, Australia
Chito		Feral	Central America, Caribbean
Tibish		Cultivated	Sudan
Acidulus		Cultivated	India, Sri Lanka
Momordica		Cultivated	India, Southeast Asia
Conomon		Cultivated	China, Japan
Makuwa	Ginmakuwa, Kanro, Ogon, Nashi-Uri, Seikan, Yuki	Cultivated	Far East
Chinensis		Cultivated	Far East
Flexuosus	Adjour, Arya, Tara	Cultivated	Morocco to India, plus northern Mediterranean
Chate		Cultivated	
Dudaim		Cultivated	Turkey to Afghanistan
Chandalak	Bucharici, Garma, Tachmi, Zami	Cultivated	Central Asia to India
Indicus		Cultivated	Central India
Ameri	Ananas, Bargi, Maculati, Mashhadi	Cultivated	Turkey to western China
Cassaba	Hassanbey, Kirkagac, Kuscular	Cultivated	West & Central Asia
Ibericus	Amarillo, Branco, Piel de Sapo, Rochet, Tendral	Cultivated	Americas, Mediterranean
Inodorus	Earl's, Honeydew	Cultivated	Japan, North & South America
Cantalupensis	American Eastern, American Western, Charentais, Ogen, Prescott, Saccharinus	Cultivated	Europe, USA

(Goldman 2004) adds additional categories for the newly developed Kabocha type (also called Buttercup), as well as Queensland and Zapallo types. To date, none of these classification schemes are supported by molecular data, nor are they globally comprehensive (Paris 2017).

Lastly, summer squash (*C. pepo*) was domesticated twice, in two independent locations; these two separate domestication events produced the two cultivated subspecies recognized today, subsp. *ovifera* and subsp. *pepo* (Paris et al. 2012). Subspecies *ovifera* includes four of the cultivar groups discussed in Section 2.4.5 (Cocozelle, Pumpkin, Vegetable Marrow and Zucchini), as well as two groups of ornamental gourds (Round Gourd and Warted Gourd) (Paris 2008); the remaining cultivar groups belong to subspecies *pepo* (i.e., Acorn, Crookneck, Scallop and Straightneck, as well as Oviform Gourds). No wild progenitor has yet been identified for subsp. *pepo*, but wild populations of subsp. *ovifera* still exist in southern USA (Chomicki et al. 2020). A third subspecies, *C. pepo* subsp. *fraterna*, grows wild in northeast Mexico; while closely related to the two cultivated subspecies, subsp. *fraterna* is not considered the progenitor of any extant cultivated forms (Kates et al. 2017).

3.3 Citrullus

The genus *Citrullus* Schrad. belongs to the tribe Benincaseae, as described by Schaefer and Renner (2011), and is hypothesized to include seven cultivated and wild species, as determined by a recent review of the taxonomy of the genus (Renner et al. 2014; Chomicki and Renner 2015). Within the genus, there is one major crop of global importance, the sweet dessert watermelon (*C. lanatus* (Thumb.) Matsum. & Nakai), as well as three minor crops of more regional importance: citron or preserving melon (*C. amarus* Schrad.), colocynth (*C. colocynthis* (L.) Schrad.) and egusi melon (*C. mucosospermus* (Fursa) Fursa). It should be noted that the nomenclature and taxonomy of the genus has yet to be fully resolved (Paris 2015; Levi et al. 2017), after a long history of confusion and taxonomic errors. For example, at various times, the citron

melon, dessert watermelon and egusi melon have all been treated as subspecies, botanical varieties and/or cultivar groups within *C. lanatus* (Paris 2015), but they are now recognized as separate species. Given that recent molecular analyses (e.g., Guo et al. 2013; Levi et al. 2013; Reddy et al. 2014; Reddy et al. 2015) have revealed genetic overlap among some of the proposed *Citrullus* species, the taxonomy may change again with the addition of further data. A recent maximum likelihood phylogeny created for *Citrullus* (Renner et al. 2019), based on 143 nuclear loci, illustrates the evolutionary relationships among currently described species; in the phylogeny, *C. mucosospermus* is sister species to *C. lanatus*.

3.4 Luffa

The genus *Luffa* Mill. belongs to the tribe Sicyoeae, as described by Schaefer and Renner (2011), and is hypothesized to include eight cultivated and wild species, as determined by a recent review of this monophyletic genus based on molecular data (Filipowicz et al. 2014). Within the genus, there are two cultivated species of importance in South and Southeast Asia: *L. acutangula* (L.) Roxb. and *L. cylindrica* (L.) M.Roem. (once commonly referred to as *L. aegyptiaca* Mill.). Table 3.3 describes the currently recognized *Luffa* species; note that some species names are not yet officially recognized (GRIN-Global 2020), and the genus generally remains poorly characterized botanically (Chomicki et al. 2020). A recent maximum likelihood phylogenetic tree for *Luffa* shows the evolutionary relationships among species (Filipowicz et al. 2014), though the tree is best approached with caution as it is based on only five loci.

3.5 Momordica

The genus *Momordica* L. is the sole member of the tribe Momordiceae, as described by Schaefer and Renner (2011). This monophyletic genus is hypothesized to contain up to 59 species, as recently proposed by Schaefer and Renner (2010) (see their Supplementary Table 1 for a full species list), with species distributed across three continents (Africa, Asia and

Table 3.3 Currently recognized *Luffa* species, as described by Filipowicz et al. (2014).

Species	Geographic distribution
Luffa acutangula (L.*) Roxb.*	Arabian Peninsula, India, Southeast Asia
Luffa astorii Svenson	Western South America (Ecuador, Peru, Venezuela)
Luffa cylindrica (L.*) M.Roem.*	Tropical Southeast Asia & Australia
Luffa echinata Roxb.	Tropical Africa (Cameroon, Chad, Ethiopia, Mali, Mauritania, Niger, Nigeria, Somalia, Sudan) & Asia (Bangladesh, India, Pakistan)
Luffa graveolens Roxb.	South-Central Asia (Bangladesh, India, Myanmar, Nepal)
Luffa operculata (L.*) Cogn.*	Northeast South America
*Luffa quinquefida (*Hook. & Arn.*) Seem.*	Central America & Mexico
Luffa saccata F.Muell. ex Naudin	Australia

Australia). However, other sources (e.g., GRIN-Global 2020) currently recognize far fewer accepted species, and the genus is in need of a thorough taxonomic revision. Within the genus, there are four cultivated species, including one major crop of global importance, the bitter gourd (*M. charantia* L.), as well as three minor crops of more local importance: balsam apple (*M. balsamina* L.), gac (*M. cochinchinensis* (Lour.) Spreng.) and spiny gourd (*M. dioica* Roxb. ex Willd.). *Momordica charantia* and *M. balsamina*, two monoecious annuals, are closely related (Bharathi et al. 2011), and fall within the same clade, named sect. *Momordica* (Schaefer and Renner 2010). The two dioecious perennials, *M. cochinchinensis* and *M. dioica*, also share a clade, named sect. *Cochinchinensis*. A recent maximum likelihood phylogenetic tree (Schaefer and Renner 2010) shows the evolutionary relationships among all 11 clades and the species they contain, though the phylogeny is based on only six loci and best approached with caution.

3.6 *Sechium/Sicyos*

The cultivated species *Sechium edule* (Jacq.) Sw. belongs to the tribe Sicyoeae, as described by Schaefer and Renner (2011); a synonym for *S. edule* is *Sicyos edulis* Jacq., as the species was classified twice simultaneously (Lira-Saade 1996). Historically, the genus *Sechium* P. Browne was regarded as well defined (see Lira-Saade 1996 for an overview) and contained 11 species in two sections, *Frantzia* and *Sechium* (Table 3.4). However, with the advent of molecular data, the tribe Sicyoeae has received renewed interest, mostly aimed at addressing long-problematic generic boundaries within the tribe. One such study (Sebastian et al. 2012) revealed that 13 smaller genera are nested within the genus *Sicyos*, including *Sechium*. The authors recommend re-circumscribing all studied species into a single, monophyletic genus; the newly enlarged genus, *Sicyos*, would contain 75 species. See the maximum likelihood phylogenetic tree created by Sebastian et al. (2012) for our most recent understanding of evolutionary relationships within this complicated group.

3.7 Other cultivated Cucurbitaceae

Other cultivated Cucurbitaceae species of regional or local importance are briefly described in Table 3.5, with naming authorities, based on information provided by Chomicki et al. (2020).

Table 3.4 Taxonomic classification of the genus *Sechium* by Lira-Saade (1996).

Section *Frantzia*	Section *Sechium*
S. panamense (Wunderlin) Lira & Chiang	*S. compositum* (J.D. Smith) C. Jeffrey
S. pittieri (Cogn.) C. Jeffrey	*S. chinantlense* Lira & Chiang
S. venosum (L.D. Gomez) Lira & Chiang	*S. edule* (Jacq.) Swartz
S. villosum (Wunderlin) C. Jeffrey	*S. hintonii* P.G. Wilson) C. Jeffrey
	S. tacaco (Pittier) C. Jeffrey
	S. talamancense (Wunderlin) C. Jeffrey

Table 3.5 Cultivated Cucurbitaceae taxa of regional and local importance, based on Chomicki et al. (2020).

Species	Common name(s)	Geographic origin	Major areas of cultivation
Benincasa hispida (Thunb.) Cogn.	Wax gourd, white gourd	Unknown	Southeast Asia, Australasia
Benincasa fistulosa (Stocks) H.Schaef. & S.S.Renner	Round gourd, tinda	Northwest India	India, Pakistan, East Africa
Coccinia grandis (L.) Voigt	Scarlet gourd, Kowai, ivy gourd	East Africa	India, Southeast Asia
Cyclanthera pedata (L.) Schrad.	Stuffing cucumber	Neotropics	South America
Hodgsonia macrocarpa (Blume) Cogn.	Lard fruit	Himalayas	China
Lagenaria siceraria (Molina) Standl.	Bottle gourd	Africa	Africa
Melothria mannii	Egusi gourd	Central America	West Africa, Neotropics
Melothria scabra Naudin	Mouse melon	Central America, Mexico	Central America, Mexico
Sicana odorifera (Vell.) Naudin	Cassabanana	South America	Latin America, Southern USA
Siraitia grosvenorii (Swingle) C.Jeffrey ex A.M.Lu & Zhi Y.Zhang	Luo Han Guo	Southern China, northern Thailand	China
Telfairia occidentalis Hook.f.	Fluted gourd	Tropical West Africa	Tropical West Africa
Telfairia pedata (Sm.) Hook.	Oyster nut	Tropical East Africa	Tropical East Africa
Trichosanthes cucumerina L.	Snake gourd	Southeast Asia	China

4 ORIGINS, DOMESTICATION AND CENTERS OF DIVERSITY

Recent advances in sequencing technologies have provided new insights into the origins and diversification of important plant families, many of which were poorly understood until the advent of molecular analyses. The Cucurbitaceae is one such family. It includes many economically important crop species (as described in Sections 2 and 3), several of which number among the world's oldest domesticates, first coming under cultivation with the dawn of agriculture some 12,000 to 10,000 years ago (Fuller et al. 2014). The origins of the family itself were recently elucidated in a multigene phylogeny, created using a global sampling of herbarium specimens (Schaefer et al. 2009). The phylogeny revealed a Southeast Asian origin, with the family evolving and initially diversifying during the Late Cretaceous. The deepest phylogenetic divergences within the Cucurbitaceae occurred some 70–80 Ma (Schaefer and Renner 2011); at this time, the Gomphogyneae, Triceratieae, Zanonieae and Actinostemmateae tribes diverged from the lineage

that gave rise to all 11 remaining tribes (previously known as the Cucurbitoideae; see Figure 1 in Renner and Schaefer 2017), which include all currently cultivated species. Since this early split, various Cucurbitaceae lineages have repeatedly spread to other continents (Africa, Americas and Australia) via the transoceanic dispersal of floating fruits, a hallmark of the family (Schaefer et al. 2009). Subsequent diversification has produced the species we know today, and the richest species diversity may now be found in the Americas (Lebeda et al. 2007).

While archaeobotanists have documented the role of Cucurbitaceae crops in ancient cultures (see Chomicki et al. 2020 for examples), new molecular data have refined estimates of domestication timelines and areas of origin, and also identified the wild ancestors and close relatives of many crops. We now know that the domestication of Cucurbitaceae species occurred early in both the Americas and in Asia (up to 11,000 years

ago for *Cucurbita* and *Lagenaria*), and more recently in Africa (at least 5,000 years ago for *Citrullus*) (Chomicki et al. 2020). Domestication occurred gradually and sometimes independently in different locations, depending on the crop. As a result of human selection, crops evolved a suite of modified traits, known as a "domestication syndrome," making them more suitable for human use and consumption than their wild relatives (Harlan 1992; Zeder et al. 2006). Depending on the species, important domestication traits in the Cucurbitaceae include increased fruit size and loss of bitterness, higher carotenoid or sugar content, increased apical dominance (i.e., less branched, more compact plants) and reduced physical defenses (such as spines). Importantly for genetic diversity, many Cucurbitaceae crops have faced more severe domestication bottlenecks than other types of crops (e.g., Qi et al. 2013).

In Sections 4.1 to 4.3, the specific origins of the most important cultivated genera and species are discussed, sorted by geographic region. Section 4.4 provides an overview of notable domestication traits in the Cucurbitaceae, with insights from recent genomic analyses.

4.1 The Americas

At present, Central and South America contain ~360 Cucurbitaceae species (Renner and Schaefer 2017), all descended from five transoceanic dispersal events, most from Africa (Schaefer et al. 2009). North American species in turn descended from these lineages as they expanded over the continent; there may have been seven such waves of expansions, as revealed by the most recent Cucurbitaceae phylogeny (Schaefer et al. 2009). In the pre-Columbian era, a number of important crops were domesticated in the Americas (Larson et al. 2014), including several species of squash and pumpkin (*Cucurbita* spp.) and also the chayote (*Sechium edule*).

4.1.1 *Cucurbita* spp.

Interestingly, the genus *Cucurbita* was once more broadly distributed than it is today, as shown by a molecular analysis of the plastid genomes of ancient, modern wild and modern cultivated *Cucurbita* taxa (Kistler et al. 2015). Adapted to the open landscapes created by large mammals in the pre-Holocene (which also likely dispersed their fruits), wild *Cucurbita* species saw a massive decline following the megafaunal extinctions and changing conditions of the Holocene. However, cultivated *Cucurbita* species showed the opposite pattern, increasing in abundance and expanding their geographic ranges as a result of domestication and human-mediated dispersal, a process that began some 10,000 years ago in modern-day Mexico (Smith 1997; Kistler et al. 2015). Today, wild *Cucurbita* species still show a center of diversity in

Mexico, though they can be found from midwestern USA to southern Argentina. The major crop species are cultivated worldwide for their edible fruits and seeds.

As discussed in Section 3.2, recent efforts using molecular data have succeeded at refining the phylogenetic tree for *Cucurbita*, dating the divergence times between lineages (Kates et al. 2017; Castellanos-Morales et al. 2018). Kates et al. (2017) produced the most robust phylogeny to date using intron sequences from 44 nuclear genes, and additionally estimated centers of origin for each of the cultivated species using extensive collection data for wild species (Figures 1 and 5 in Kates et al. 2017). Castellanos-Morales et al. (2018) used six chloroplast loci to estimate diversification rates, in addition to tree topology and divergence times (Figure 3 in Castellanos-Morales et al. 2018). The two tree topologies are largely identical, except that the placement of the clade containing *C. argyrosperma* and *C. moschata* varies slightly. Overall, the genus diverged from its sister lineage (*Peponopsis adhaerens*) roughly 11.24 Ma, with some sister species within the genus diverging as recently as 0.35 Ma (*C. lundelliana* and *C. okeechobeensis* subsp. *martinezii*) (Castellanos-Morales et al. 2018).

Among the major crops, ***C. argyrosperma* subsp. *argyrosperma*** (the cushaw) and ***C. moschata*** (butternut squash) are sister species. The domestication of *C. argyrosperma* subsp. *argyrosperma* likely occurred in Mexico, where the species is native (Sanjur et al. 2002), but this is not currently supported by archaeological remains (Chomicki et al. 2020). Its domestication history requires further study, especially as subsp. *argyrosperma* and subsp. *sororia* (the putative wild progenitor) accessions were intermixed in the phylogeny of Kates et al. (2017), suggesting a complex history of multiple centers of diversification, a broad domestication bottleneck or ongoing crop-wild introgression. The wild progenitor of *C. moschata* has yet to be identified, and its origins also remain in doubt. Initial hypotheses supported a South American origin for *C. moschata* (in Colombia; Nee 1990), as suggested by high local landrace diversity and the presence of landraces with primitive traits. However, molecular studies have placed *C. moschata* in the North American/Central American clade, and suggested instead a potential shared domestication history with *C. argyrosperma* (Sanjur et al. 2002; Zheng et al. 2013; Kistler et al. 2015; Kates et al. 2017; Castellanos-Morales et al. 2018).

The sister group to *C. argyrosperma* + *C. moschata* in the phylogeny of Kates et al. (2017) comprises accessions from ***C. pepo*** (summer squash), another major cucurbit crop. Evidence from a number of sources supports two domestication events for *C. pepo* (Smith 1997; Sanjur et al. 2002; Paris et al. 2012): an initial

domestication in Mexico some 8,000–10,000 years ago (*C. pepo* subsp. *pepo*), and a subsequent independent domestication in southeastern USA roughly 5,000 years ago (*C. pepo* subsp. *ovifera*). The wild progenitor of *C. pepo* subsp. *pepo*, the more widely cultivated subspecies, remains elusive. Molecular studies (e.g., Kates et al. 2017; Castellanos-Morales et al. 2018) have hypothesized a complex domestication history, but the particulars remain contentious, in particular the role (if any) of the wild subspecies *fraterna*, which some authors have suggested as a potential wild progenitor (Castellanos-Morales et al. 2019). In the case of subsp. *ovifera*, wild populations are known to exist in the US state of Texas, but, similarly to the case with *C. argyrosperma* subsp. *argyrosperma*, these wild accessions were intermixed with cultivated ones in the molecular phylogenies (Kates et al. 2017), also suggesting a need for further study (and potentially broader sampling) to clearly resolve the domestication history.

Cucurbita maxima is sister species to the wild species *C. ecuadorensis*, and together they form a sister group to the clade comprising the other major cucurbit crops (Kates et al. 2017; Castellanos-Morales et al. 2018). Molecular analyses have confirmed that ***Cucurbita maxima* subsp. *maxima*** (pumpkin, winter squash) was domesticated only once in southern South America (likely in modern-day Argentina) more than 4,000 years ago from its wild ancestor subsp. *andreana* (Sanjur et al. 2002; Kates et al. 2017). While long cultivated in South America, *C. maxima* subsp. *maxima* does not appear to have left the Neotropics during the pre-Columbian era (Chomicki et al. 2020), unlike other cucurbit crops.

Lastly, the placement of ***Cucurbita ficifolia*** (fig-leaf gourd), a minor crop within the genus, within the *Cucurbita* phylogeny has long been debated, as its position tends to vary among gene trees (i.e., incomplete lineage sorting) and those of different molecular studies (Zheng et al. 2013; Paredes-Torres 2016; Kates et al. 2017). However, the most recent such studies (Kates et al. 2017; Castellanos-Morales et al. 2018) have placed *C. ficifolia* as sister to the rest of the mesophytic species, though more extensive sampling is needed to confirm this placement. The wild progenitor of *C. ficifolia* remains unknown, and the only reliable archaeological records come from western South America, making this the most likely center of origin (Sauer 1993; Sanjur et al. 2002).

4.1.2 *Sechium edule*

Sechium edule (chayote) was also domesticated in the Americas, most likely in modern-day Mexico and Guatemala, as initially determined by historical and linguistic studies, and suggested by high cultivar genetic diversity in this area (Newstrom 1991; Chomicki et al.

2020). This hypothesis is also supported by a recent biogeographic study (Sebastian et al. 2012) that reconstructed the history of the tribe Sicyoeae using plastid and nuclear DNA sequences from 87 species; here, Mexico was found to be the ancestral area of the clade. Wild forms of *S. edule* exist in Mexico, and populations from La Esperanza and Tetla represent the best candidates for the wild progenitor, owing to their small, heavily-spined fruits (both primitive traits) (Newstrom 1991). Costa Rica has also been identified as a secondary center of chayote diversity (Cross et al. 2006), and the crop is now widely grown across Africa, southern Europe and Asia, following its introduction in the 19th century.

4.2 Africa

At present, the African continent hosts some 25 genera of Cucurbitaceae (Renner and Schaefer 2017), all descended from seven transoceanic dispersal events: five from Asia and two from America (Schaefer et al. 2009). Ancestral African lineages then colonized Madagascar at least 13 times, where the family has since greatly diversified into some 50 species. The most important crop species to be domesticated in Africa are those belonging to the genus *Citrullus*, such as dessert watermelon (*C. lanatus*).

4.2.1 *Citrullus* spp.

As discussed in Section 3.3, there is one major *Citrullus* crop, **C. lanatus** (watermelon), as well as three minor crops in the genus: **C. amarus** (citron or preserving melon), **C. colocynthis** (colocynth) and **C. mucosospermus** (egusi melon). The phylogenetic relationships among these cultivated species and the three wild *Citrullus* species (*C. ecirrhosus*, *C. naudinianus* and *C. rehmii*) have recently been resolved (Renner et al. 2019). In an attempt to clarify the origins of domesticated *C. lanatus* (which have long remained shrouded in mystery), Renner et al. (2019) skimmed genome data for all seven currently recognized *Citrullus* species, as well as a 3,560-year-old leaf sample from an Egyptian mummy's sarcophagus; to assemble the phylogeny, complete plastid genomes as well as 143 single-copy nuclear gene sequences were used. The structure of the phylogeny (Figure 2 in Renner et al. 2019) was as follows: (((((C. lanatus + C. mucosospermus), C. amarus), C. ecirrhosus), C. rehmii), C. colocynthis) + C. naudinianus*. This revealed that *C. naudinianus* was sister to a clade containing all other species in the genus.

Part of the confusion regarding the origins of *C. lanatus* may have resulted from the misidentification of a type specimen originally described in present-day South Africa by a student of Linnaeus (in 1773). With the advent of molecular analyses, this

misidentification was brought to light, and the type specimen properly identified as *C. amarus* (and not *C. lanatus*), helping to resolve many taxonomic issues within the genus (Chomicki and Renner 2015). Molecular data have also identified *C. mucosospermus* as the sister species of *C. lanatus* (Chomicki and Renner 2015; Renner et al. 2019) and have supported northeastern Africa as the most likely center of origin, a hypothesis also supported by archaeological and historical data (Chomicki et al. 2020). Indeed, the ancient leaf sample tested by Renner et al. (2019) proved to be from a red-fleshed, sweet melon, genetically similar to watermelon. While the wild progenitor of watermelon remains undescribed, one candidate is *C. lanatus* subsp. *cordophanus*, the white-fleshed Sudanese Kordophan melon, which was the closest relative to *C. lanatus* in Renner et al.'s (2019) molecular phylogeny. However, given the lack of bitterness and high sugar content of the Kordophan melon, it may also represent a landrace or early traditional variety (Chomicki et al. 2020).

In contrast to watermelon, which is cultivated for its sweet fruit flesh, its sister species *C. mucosospermus* was domesticated for its nutritious seeds (Achigan-Dako et al. 2015). *Citrullus mucosospermus* originated in western Africa, where wild, semi-cultivated and cultivated forms have been documented (Jeffrey 2001). However, little information is available on the timeline of its domestication. Similarly, another minor crop, *C. amarus*, originated in southern Africa, where wild forms are known (Chomicki et al. 2020), but little is known of its original domestication in Africa. Beginning in the Roman era (or even earlier), the crop was dispersed to the Mediterranean region, where it flourished; both archaeological and iconographic evidence support its wide cultivation in this region from the 14th century onwards (Paris et al. 2013; Paris 2015). Also introduced to Australia for use as fodder, *C. amarus* may still be found there as a weed (Shaik et al. 2017). Lastly, *C. colocynthis* originated in northern Africa, and is not considered to be a domesticated species (Chomicki et al. 2020); wild forms have been grown for medicinal purposes and as a source of oil for at least the past 5,000 years, as supported by archaeological evidence from Libya, Egypt and the Near East (Wasylikowa and Van Der Veen 2004).

4.3 Asia and Melanesia

As previously described, the Cucurbitaceae family first evolved and diversified in Southeast Asia, where some clades remain extant today (Schaefer et al. 2009). Additionally, other clades that diversified on other continents later returned to Asia, a testament to the dispersal capabilities of the family. The crop species domesticated in Asia are varied, and include major crops such as cucumber and muskmelon (both *Cucumis* species), a number of gourd species (*Benincasa hispida*, *Lagenaria siceraria*, *Luffa* spp. and *Momordica charantia*) and several minor crop species. Interestingly, some species originated elsewhere, prior to domestication in Asia. Appendix VIII provides further information on the Cucurbitaceae in India, an important center of diversity.

4.3.1 *Cucumis* spp.

While the genus *Cucumis* contains two major global crops, *C. melo* (muskmelon) and *C. sativus* (cucumber), research into these and other *Cucumis* species was long hampered by the lack of an accurate and comprehensive phylogeny for the genus. In 2007, molecular studies revealed that *Cucumis*, as originally described (based on morphological data), was not monophyletic (Ghebretinsae et al. 2007; Renner et al. 2007), and the genus was redefined to include members of the former genera *Dicaelospermum*, *Mukia*, *Mymecosicyos* and *Oreosyce*. Such ongoing taxonomic issues have meant that the domestication history of *Cucumis* crops has only been described very recently; in particular, that of muskmelon was only revised with the publication of novel molecular analyses in the last few years (Endl et al. 2018; Zhao et al. 2019). As such, these findings remain under scrutiny by the larger scientific community, raising the possibility of further refinements. As a genus, *Cucumis* remains relatively understudied, and poorly collected and characterized.

Of Asian origin, *Cucumis sativus* is most closely related to the wild species *C. hystrix*, with the split between these two sister species dated to 3 Ma (Endl et al. 2018). For comparison, the genus *Cucumis* diverged from its African relatives approximately 12–13 Ma (Sebastian et al. 2010; Endl et al. 2018). Domesticated cucumbers (*C. sativus* var. *sativus*) are derived from *C. sativus* var. *hardwickii*, which was identified as the wild progenitor using a combination of linguistic and genetic evidence (Sebastian et al. 2010; Qi et al. 2013). The wild progenitor occurs naturally throughout India and Thailand, and produces small, bitter fruits (Chomicki et al. 2020). Domestication took place some 2,500 years ago on the Indo-Gangetic plain, an area that shows particularly rich genetic diversity for *C. sativus*, and was accompanied by a severe domestication bottleneck (Qi et al. 2013). As discussed in Section 3.1, three genetic groups of cultivars were later selected for different purposes. Eurasian cucumbers, or "slicing cucumbers," are typically harvested immature and eaten raw, while East Asian cucumbers are pickled (Chomicki et al. 2020). Xishuangbanna cucumbers (*C. sativus* var. *xishuangbannanensis*) were selected for high beta-carotene content and may be eaten both immature and mature (Renner 2017).

Many of the details of the domestication history of *Cucumis melo* remain uncertain, but molecular evidence strongly supports at least two independent domestication events (Endl et al. 2018; Zhao et al. 2019): one or more Asian (***C. melo* subsp. *melo***) and one African (***C. melo* subsp. *meloides***). The lineages that gave rise to these two geographic subspecies diverged at least 2 Ma. However, precise estimates of the domestication timeline are yet to be obtained for either lineage, although archaeological evidence suggests domestication occurred at least 3,000 years ago (Chomicki et al. 2020). Today, all modern cultivars belong to the Asian lineage, subsp. *melo*, including commercially important groups such as 'Cantalupensis' and 'Inodorus' (as described in Section 3.1). The African lineage includes the Sudanese group Tibish and likely the African Fadasi and Seinat landraces, which are of local importance only. While many subsp. *meloides* landraces are still grown in North Africa, they are threatened with replacement by higher-yielding, modern cultivars from Asia. As such, African landraces (belonging to subsp. *meloides*), as well as wild African melons, represent a potentially rich source of genetic diversity that is currently poorly collected or described. The closest relatives of *C. melo*, the Australian *C. picrocarpus* and Indian perennial *C. trigonus*, also represent important sources of diversity (Endl et al. 2018). These closely related species, which diverged ~3 Ma from *C. melo*, may be valuable for breeding efforts, particularly *C. trigonus*, which is a drought-tolerant species.

4.3.2 *Benincasa hispida*

The origins of *Benincasa hispida* (wax gourd) remain largely undescribed, with no molecular studies to date. Today, wax gourd is cultivated mainly in Southeast Asia and Australasia (Chomicki et al. 2020), but the place of domestication is undetermined, although wild forms (long elusive) have been described from Australia, Japan and parts of Melanesia (Marr et al. 2007). Archaeological finds place wax gourds in Thailand nearly 10,000 years ago (Pyramarn 1989) and in New Guinea 2,450 years ago (Matthews 2003), with seed size within the range of domesticated forms. A related minor crop, *Benincasa fistulosa*, is cultivated in India and Pakistan, where wild forms also exist (Renner and Pandey 2013).

4.3.3 *Lagenaria siceraria*

Lagenaria siceraria (bottle gourd) is originally native to Africa; where wild populations still exist in present-day Zimbabwe (Decker-Walters et al. 2004), but it was domesticated twice in completely different parts of the world: once in East Asia and once in the Americas (Chomicki et al. 2020). Among the world's

earliest crops, bottle gourds were in use in East Asia as early as 11,000 years ago (Kistler et al. 2014), and up to 10,000 years ago in the Americas, as indicated by archaeological data (Erickson et al. 2005). The dispersal of domesticated bottle gourds to the Americas from East Asia was long a mystery, as transport by humans would involve tolerance to cold Arctic climates. The mystery was solved by Kistler et al. (2014), who used plastid DNA sequences to describe patterns of relatedness among both ancient and extant bottle gourds; all pre-Columbian bottle gourds were more closely related to African gourds than Asian gourds, suggesting that wild *L. siceraria* naturally dispersed to the Americas via transoceanic currents, likely during the late Pleistocene. Similarly, molecular data have revealed East Asian and American origins for bottle gourds from Polynesia, dispersal events that also may have been natural, though human-mediated dispersal cannot be excluded (Clarke et al. 2006).

4.3.4 *Luffa* spp.

As discussed in Section 3.4, the genus *Luffa* is currently hypothesized to include eight species (Filipowicz et al. 2014), including two minor crops, *L. acutangula* (angled loofah) and *L. cylindrica* (smooth loofah). As reviewed by Filipowicz et al. (2014), experts have long disagreed on the number of *Luffa* species and species delineations, and these taxonomic issues have limited our understanding of the genus. In the latest molecular phylogeny (Filipowicz et al. 2014), *C. acutangula* is the sister group of a clade comprising the remainder of the *Luffa* species, while *L. cylindrica* is sister to *L. saccata*, a wild species from Australia. To date, virtually nothing is known regarding the domestication history of the two loofah crops (Chomicki et al. 2020). Wild forms of *L. acutangula* occur on the Arabian Peninsula and in India (Filipowicz et al. 2014), and small-fruited wild forms of *L. cylindrica* occur in Australia and Indonesia (Marr et al. 2005).

4.3.5 *Momordica* spp.

The genus *Momordica* today is hypothesized to comprise nearly 60 species, though many have yet to be fully accepted (see discussion in Section 3.5). The majority of the species are distributed in Africa, with the remainder occurring in Australasia (Schaefer and Renner 2010). Constructed using molecular data (Schaefer and Renner 2010), the latest phylogeny for the genus supports an African origin (for the genus), with the Asian species a result of a single dispersal event, ~19 Ma. *Momordica* contains the major cucurbit crop, *M. charantia* (bitter gourd), as well as three minor crops: *M. balsamina* (balsam apple), *M. cochinchinensis* (gac) and *M. dioica* (spiny gourd). Within the molecular phylogeny (Schaefer and

Renner 2010) discussed in Section 3.5, *M. balsamina* and *M. charantia* are closely related and both belong to the section *Momordica*, while *M. cochinchinensis* and *M. dioica* are also closely related and belong to the section *Cochinchinensis*. As highlighted in Section 2.5.3, among the minor crops, only *M. cochinchinensis* shows evidence of domestication, which has yet to be described.

Momordica charantia is native to Africa, but widely cultivated in South Asia, where it forms an important part of the cuisine (Chomicki et al. 2020). The origins of bitter gourd domestication remain a matter of debate, but the strongest evidence to date is for a South Asian origin (Matsumura et al. 2019), though this will require further sampling of landraces and wild populations across the range to confirm. In this regard, India may be considered as an important center of diversity, on the basis of historical accounts (Walters and Decker-Walters 1988; Chakravarty 1990) and recent molecular analyses (Singh et al. 2007; Gaikward et al. 2008). According to a recent genomic analysis (Matsumura et al. 2019), which re-sequenced 61 cultivated and wild accessions to identify South Asia as the site of domestication, cultivated bitter gourds first diverged from their wild progenitors 6,000 years ago. The study was unable to identify strong candidate genes for domestication, suggesting a non-traditional model of domestication (e.g., with intermittent, weak selection, and/or highly polygenic domestication traits).

4.4 Cucurbitaceae domestication

Domestication refers to the process of adapting wild plant species for human use. For any species, this process occurs gradually (often over thousands of years) and may occur over large geographic areas, in some cases completely independently (Meyer et al. 2012). Given the lengths of time involved, plant species currently under cultivation may vary in the extent, or level, of domestication (Dempewolf et al. 2008). Eventually, domestication produces a series of phenotypic (and underlying genetic) changes that distinguish a crop from its wild progenitor; this suite of modified traits is referred to as the "domestication syndrome." The particular traits comprising the domestication syndrome can vary among taxa, but commonly crop plants exhibit increases in fruit/grain size, a loss of bitterness in edible structures (among other changes to secondary metabolites), a loss of shattering (i.e., loss of seed dispersal) as well as of seed dormancy, and increased apical dominance (i.e., reduction in branching) (Hammer 1984; Harlan 1992; Stetter et al. 2017). In the case of Cucurbitaceae crops, domestication almost always involved a loss of bitterness (Zhou et al. 2016), although there is one exception:

the bitter gourd (Marr et al. 2004). Other important domestication traits include sweetness (higher sugar content), larger fruits and higher carotenoid content (Chomicki et al. 2020).

With the advent of molecular data and analyses, the genetic basis of domestication traits and mechanisms underlying the domestication process are coming to light. Questions on crop origins and diversification, patterns of selection and domestication bottlenecks, and how domestication patterns vary among species have all seen fascinating insights using genetic and genomic datasets. While initial studies of domestication focused on "model" crops, such as maize (e.g., see review by Doebley et al. 2006), recent advances in sequencing technologies have allowed a broad range of plant species to be examined (e.g. 203 diverse food crops in a recent Tansley review: Meyer et al. 2012). The Cucurbitaceae are no exception to this trend, and genomes have now been produced for a number of major crops under the auspices of the Cucurbit Genomics Project by CucCAP. Reference genomes of varying qualities are available for four cultivated *Cucurbita* species (*C. argyrosperma*, *C. maxima*, *C. moschata* and *C. pepo*); cultivated cucumber (*Cucumis sativus* var. *sativus*) and its wild progenitor (*C. sativus* var. *hardwickii*); muskmelon (*Cucumis melo*); watermelon (*Citrullus lanatus*); bottle gourd (*Lagenaria siceraria*) and wax gourd (*Benincasa hispida*). These, and other molecular resources, are providing new insights into Cucurbitaceae crop domestication, which are summarized below.

4.4.1 Loss of bitterness

The majority of wild cucurbits have bitter fruits, an anti-herbivory trait conferred by high levels of cucurbitacins (Chomicki et al. 2020). As discussed above, the loss of bitterness was an important initial domestication trait for most Cucurbitaceae fruit crops (as opposed to those few species cultivated for their seeds, such as egusi melon). Biochemical studies have revealed that different categories of cucurbitacins (C, B and E) are responsible for bitterness in cucumber, muskmelon and watermelon, respectively (Lester 1997; Matsuo et al. 1999; Shang et al. 2014). In cucumber, fruit bitterness is conferred by the *Bt* allele, which encodes a transcription factor crucial to the biosynthesis of cucurbitacin C. During domestication, a mutation in the *Bt* promoter downregulated its production, causing the loss of bitterness in cucumber fruits, as revealed by comparisons among accessions varying in bitterness (Shang et al. 2014). Interestingly, a strong selective sweep was observed at the *Bt* locus, but not at the related *Bl* locus (which confers leaf bitterness), suggesting that leaf bitterness was selectively preserved (Qi et al. 2013). In a comparative genomic anal-

ysis (Zhou et al. 2016), independent mutations within syntenic transcription factor genes (for cucumber *Bt*) in muskmelon and watermelon were found to reduce fruit bitterness, a sign of convergent domestication among these three crops (i.e., domestication used the same pathway). The fact that the major gene clusters for cucurbitacin biosynthesis are highly conserved among species also suggests historical selection pressures on these loci to stabilize the production of cucurbitacins.

4.4.2 Selection for sweetness

Independently from loss of bitterness, selection for increased sugar content was also a common feature of cucurbit domestication, particularly for muskmelon and watermelon (Chomicki et al. 2020). Genomic and transcriptomic analyses in both species have revealed a plethora of sugar metabolism and transporter genes potentially involved in regulating flesh sweetness (Garcia-Mas et al. 2012; Guo et al. 2013; Guo et al. 2015). By comparing sweet dessert watermelon (*C. lanatus*) to semi-sweet egusi melon (*C. mucosospermus*) and non-sweet colocynth (*C. colocynthis*), Guo et al. (2019) were able to demonstrate a selective sweep for an alkaline galactosidase gene, *Cla97C04G070460* (*ClAGA2*), most likely involved in the evolution of greater flesh sweetness. Similarly, the sugar transporter ClTST2 was shown to be selected for both during watermelon domestication and improvement. A role for ClTST2 in watermelon domestication was also suggested by a mapping study using 96

recombinant inbred lines, derived from crossing sweet and unsweet accessions (Ren et al. 2018). Thus, sweetness has likely resulted from selection on a diversity of genes and, interestingly, there is some indication that selection for sweetness and red color (i.e., higher carotenoid content) may have occurred concurrently (Zhang et al. 2017).

4.4.3 Selection for larger fruits and high carotenoid content

Selection for larger fruits is a common feature of cucurbit crop domestication. The regulation of fruit size is a complex process, not always well understood, and preliminary results from different cucurbit crops suggest idiosyncratic pathways were utilized during domestication for fruit size (see Chomicki et al. 2020 for a review). Even among closely related cultivated species, such as the three *Citrullus* crops, fruit size enlargement was likely achieved in unique ways. For example, quantitative-trait locus (QTL) mapping revealed different, but overlapping, sets of QTLs among the three species (Guo et al. 2019). The same is true of selection for high carotenoid content (orange or red fruit pulp), usually in the form of beta-carotene or lycopene. Studies, predominantly from muskmelon and watermelon (though the Xishuangbanna cucumber has also been examined), tend to identify a diversity of enzymes and transcription factors involved in the carotenoid biosynthetic pathway, both within and among species.

5 CROP GENE POOLS

The processes of crop domestication and improvement have resulted in substantial decreases in genetic variation for most cultivated species, limiting efforts at further improvement in the face of challenges such as climate change (Doebley et al. 2006; Flint-Garcia 2013). As such, crop wild relatives (CWRs, including wild progenitors) represent essential sources of genetic diversity, invaluable to agriculture. Used for many decades in crop breeding, CWRs have served as important reservoirs of diversity for abiotic stress tolerance, disease and pest resistance, and nutritional and yield-enhancing traits, among other agronomically important traits (Castañeda-Álvarez et al. 2016; Dempewolf et al. 2017). Nonetheless, uncovering such useful traits among a plethora of CWRs can prove costly and challenging, and once discovered, there are many difficulties inherent in moving underlying beneficial alleles into cultivated species, especially from more distant CWRs.

To this end, the categorization of CWRs based on their ease of hybridization with the crop and an assessment of their potential for use in breeding programs is crucial to facilitate breeding efforts (Miller and Khoury 2018). As proposed by Harlan and De Wet (1971), the concept of crop gene pools (i.e., the sum total of all genetic resources within an interbreeding population) has been widely applied to categorize CWRs on the basis of crossability with the crop species. In this system, the gene pool is divided into primary, secondary and tertiary gene pools, as follows:

1. **Primary gene pool:** consists of the crop species, as well as any conspecific taxa that are fully cross-compatible with the crop (including cultivated, wild and weedy forms).
2. **Secondary gene pool:** consists of all related species (usually congeners) that are capable of crossing with the crop species, despite the presence of some genetic barriers. For example, the resulting hybrids may have poor vigor or reduced fertility.
3. **Tertiary gene pool:** consists of more distantly related species for which there are substantial genetic barriers to hybridization. Gene transfer is still possible, but with great difficulty, for example by using special biotechnological tools (e.g., embryo rescue) or advanced breeding techniques such as bridging crosses (with intermediate species).

Historically, crossing experiments were used to determine the species composition of the secondary and tertiary gene pools for a given crop. However, these are expensive and time consuming, and more recent approaches have begun to use information on evolutionary relationships to understand patterns of interspecies fertility (Miller and Khoury 2018). In this section, the current state of knowledge for the gene pools of the major Cucurbitaceae crops is presented.

5.1 *Cucumis*

As discussed in previous sections, the genus *Cucumis* includes two major crops, *C. melo* (melons) and *C. sativus* (cucumber), among more than 50 constituent species. Although both crop species belong to the same subgenus, *Cucumis* (Schaefer 2007; Li et al. 2011), recent molecular phylogenetic studies (e.g., Chung et al. 2006; Renner et al. 2007; Sebastian et al. 2010) have shown these two crop species to be fairly distantly related, with their respective lineages diverging some eight million years ago (Endl et al. 2018). The two crops also possess different numbers of chromosomes (see Sections 2.1 and 2.3), and crossing experiments have confirmed the early abortion of embryos from attempted *C. melo* × *C. sativus* crosses (Kirkbride 1993). Within the genus, species tend to cluster phylogenetically according to geography, with Asian (and Australian) species largely separate from African species. Early crossing experiments have shown varying levels of compatibility among *Cucumis* species (e.g., van Raamsdonk et al. 1989; Kirkbride 1993), with geographically proximal species more likely to hybridize successfully.

5.1.1 *Cucumis melo*

Wild forms of *C. melo* are found in Africa, Asia and Australia, and early efforts to understand muskmelon's domestication history variously placed its origins in Africa and Asia (Sebastian et al. 2010). Evidence for an African origin included shared cytological characteristics between *C. melo* and other African *Cucumis* species, while the high genetic diversity seen in East Asian muskmelon landraces tended to support an Asian origin. However, as reviewed in Section 4.3.1, advocates of both African and Asian origins were correct, and recent molecular evidence supports at least two independent domestication events (Endl et al. 2018; Zhao et al. 2019): one in Africa (from *C. melo* subsp. *meloides*, as named by Endl et al. 2018) and one in Asia (from *C. melo* subsp. *melo*). Together, these two subspecies, containing both cultivated and wild forms of *C. melo*, comprise the primary gene pool of muskmelon.

To date, no concrete attempts have been made to define the secondary and tertiary gene pools for muskmelon. However, the closest relatives of *C. melo* are the two species in its sister group: *C. picrocarpus* (Australia) and *C. trigonus* (India) (Endl et al. 2018). Long missed due to taxonomic confusion, the recent rediscovery (and accurate characterization) of *C. trigonus* has suggested the possibility of other overlooked CWRs from Southeast Asia, ready to be discovered with denser sampling of this understudied region (from India to Australia). Crossing attempts between *C. melo* cultivars and *C. trigonus* have been successful (Joseph John et al. 2013), and it is believed the same will be true for *C. picrocarpus* (Endl et al. 2018), though such experiments have not yet been made. Interspecific crosses in *Cucumis* remain extremely challenging, as compared to other genera with weaker species boundaries (Chen and Adelberg 2000), and these discoveries will pave the way to introduce beneficial traits from wild species into cultivated muskmelon.

5.1.2 *Cucumis sativus*

Cucumis sativus contains three botanical varieties: cultivated cucumber (*C. sativus* var. *sativus* and var. *xishuangbannanensis*) and the wild progenitor (*C. sativus* var. *hardwickii*). Together, these comprise the primary gene pool for cucumber, and the varieties are fully interfertile (Lebeda et al. 2007; Renner 2017). Native to India, populations of the wild progenitor grow in sympatry there with cultivated cucumber (in the Himalayan foothills). In northern India, there is also evidence of fairly recent introgression from *C. sativus* var. *hardwickii* into var. *sativus* landraces (Horejsi and Staub 1999). Compared to the wild progenitor, cultivated cucumber is genetically depauperate, and there is evidence of a particularly severe domestication bottleneck for cucumber, on par with that seen for other fruit species (Qi et al. 2013). Apparently, only a small fraction of the genetic diversity in the wild progenitor was captured in domesticated forms (Lv et al. 2012), thus *C. sativus* var. *hardwickii* represents a potentially rich resource of novel alleles for cucumber breeding.

The closest relative of *C. sativus* is *C. hystrix*, its sister species (Sebastian et al. 2010; Endl et al. 2018) and a member of the secondary gene pool of cucumber (Lebeda et al. 2007). The first cross to be made between a cultivated *Cucumis* species and a wild species (Chen and Adelberg 2000), the pollination of *C. sativus* by *C. hystrix* followed by embryo rescue repeatedly produces F$_1$ hybrids. From this cross, the fully fertile, amphidiploid species *C. hytivus* was created (Chen et al. 1997; Chen et al. 1998), which can be backcrossed to *C. sativus* to produce diploid progeny, a potentially highly useful approach for cucumber improvement (Staub and Delannay 2011). Otherwise, the secondary gene pool of cucumber remains poorly defined, potentially including a number of cross-incompatible wild congeners (Naegele and Wehner 2017). This is also the case for the tertiary gene pool, which is currently thought to include more distantly related *Cucumis* species (e.g., those in the subgenus *Humifructus*) and species in other genera (e.g., *Cucurbita*) (Naegele and Wehner 2017). While wild *Cucumis* species represent an important source of useful traits for cucumber breeding (especially, e.g., pathogen resistance), this diversity has been difficult to access, owing to limited success with interspecific hybridization compared to other genera (Chen and Adelberg 2000).

5.2 *Cucurbita*

The genus *Cucurbita* includes five cultivated species (*C. argyrosperma, C. ficifolia, C. maxima, C. moschata* and *C. pepo*) and 10 additional wild species, as described in previous sections. These may be placed into seven groups, as shown in Table 5.1; these groups were created on the basis of traditional classification schemes updated with the latest evolutionary findings. For example, recent molecular analyses have elucidated patterns of relatedness among species in robust, well-supported phylogenies (Kates et al. 2017; Castellanos-Morales et al. 2018). The cultivated *Cucurbita* species are reproductively isolated from one another, though barriers to hybridization are incomplete and experimental crosses can be made with difficulty (Lebeda et al. 2007). Low crossability is a particular challenge in *Cucurbita*, compared to other genera with cultivated species, which limits the ability to move agronomically beneficial traits from one species to another. The success of interspecific hybridizations may be increased by using genetic bridges, by increasing gametic diversity or by selecting particular accessions. For example, Gong et al. (2013) described substantial variation in the genetic distance between pairs of accessions from different *Cucurbita* species, and a lower genetic distance may be predictive of success in interspecific crosses.

Natural hybridization among the cultivated *Cucurbita* species is rare, but does occur; these natural interspecific hybrids have mostly been reported among Mexican landraces (Decker-Walters et al. 1990; Merrick 1991). Crossing experiments have revealed varying levels of compatibility among cultivated species, with *C. moschata* generally having the best crossability with congeneric species (OECD 2016). The gene pools of each of the five cultivated species are discussed below (summarized in Table 5.2). Note that some of the specifics remain open to debate.

Table 5.1 List of *Cucurbita* taxa illustrating their group membership and natural distributions.

Cucurbita group	Included taxa	Natural distribution
Argyrosperma	*C. argyrosperma* C. Huber *C. moschata* Duchesne	Southwestern USA, Mexico, Mesoamerica Central America, Mexico
Digitata	*C. cordata* S. Watson *C. digitata* A. Gray *C. palmata* S. Watson	Mexico Mexico, USA Mexico, USA
Ficifolia	*C. ficifolia* Bouché	Mexico, western South America
Foetidissima	*C. foetidissima* Kunth *C. pedatifolia* L.H. Bailey *C. radicans* Naudin *C. scabridifolia* L.H. Bailey	Mexico, USA Central Mexico Mexico Northeastern Mexico
Maxima	*C. ecuadorensis* H.C. Cutler & Whitaker *C. maxima* Duchesne	Ecuador South America
Okeechobeensis	*C. lundelliana* L.H. Bailey *C. okeechobeensis* (Small) L.H. Bailey	Central America, Mexico Southern USA, Mexico
Pepo	*C. pepo* L.	Southern USA, Mexico

Source: Distribution data adapted from OECD (2016).

Table 5.2 The gene pools of the five cultivated *Cucurbita* species.

	Primary gene pool	Secondary gene pool	Tertiary gene pool
C. argyrosperma	*C. argyrosperma* subsp. *argyrosperma* subsp. *sororia* (L.H. Bailey) Merrick & D.M. Bates	*C. moschata*	*C. foetidissima* *C. maxima* *C. pepo*
C. ficifolia	*C. ficifolia*	*C. foetidissima* *C. pedatifolia*	*C. lundelliana* *C. maxima* *C. pepo*
C. maxima	*C. maxima* subsp. *andreana* (Naudin) I.A. Filov subsp. *maxima*	*C. ecuadorensis*	*C. argyrosperma* *C. ficifolia* *C. lundelliana* *C. pepo*
C. moschata	*C. moschata*	*C. argyrosperma*	*C. lundelliana* *C. maxima* *C. pepo*
C. pepo	*C. pepo* subsp. *fraterna* (L.H. Bailey) Lira et al. subsp. *ovifera* (L.) D.S. Decker subsp. *pepo*	*C. argyrosperma* *C. ecuadorensis* *C. moschata* *C. okeechobeensis*	*C. ficifolia* *C. lundelliana* *C. maxima*

Source: Summary based on crossability studies by Lebeda et al. (2007)

5.2.1 *Cucurbita argyrosperma*

The primary gene pool of *C. argyrosperma* includes two interfertile subspecies: *C. argyrosperma* subsp. *argyrosperma* (the cultivated form, or cushaw) and *C. argyrosperma* subsp. *sororia* (the wild form and progenitor). The cultivated and wild subspecies occur sympatrically in parts of the range, and natural hybrids are a frequent occurrence (Merrick 1991). Based on hybridization studies, *C. argyrosperma* crosses most easily with *C. moschata*, placing it into the secondary gene pool of cushaw (Lira-Saade 1995). As noted in Sections 3 and 4, *C. moschata* has been shown to be the sister species of *C. argyrosperma* in the latest molecular phylogenies (Kates et al. 2017; Castellanos-Morales et al. 2018). According to Lira-Saade (1995), the next level of cross-compatibility (and hence tertiary gene pool) includes the wild perennial *C. foetidissima*, *C. maxima* cultivars, and cultivated and wild forms of *C. pepo*.

5.2.2 *Cucurbita ficifolia*

The gene pool of fig-leaf gourd (*C. ficifolia*) is somewhat more problematic to define, as among the cultivated species, *C. ficifolia* shows the strongest hybridization barriers with other congeneric species. In experimental settings, interspecific hybrids have been made between *C. ficifolia* and three other wild species: *S. foetidissima, C. pedatifolia* and, to a lesser extent, *C. lundelliana* (Lira-Saade 1995). On this basis, these species have been placed in cushaw's secondary and tertiary gene pools, respectively, as the hybrids are difficult to achieve and typically low in fertility. Of particular note is *C. lundelliana*, as Whitaker (1959, 1962) discovered broad compatibility between this wild species and cultivated *Cucurbita* species, meaning it might serve as a bridging species in interspecific crosses.

5.2.3 *Cucurbita maxima*

The primary gene pool of *C. maxima* includes two interfertile subspecies: *C. maxima* subsp. *andreana* (the wild form and progenitor) and *C. maxima* subsp. *maxima* (the cultivated form, pumpkin/winter squash). As noted for *C. argyrosperma*, the cultivated and wild subspecies of *C. maxima* naturally co-occur in parts of the range, and genetic interchange occurs frequently between the two (Merrick 1991). In the *Cucurbita* phylogeny (Kates et al. 2017), *C. maxima* and *C. ecuadorensis* are sister species (forming a South American clade), and, interestingly, crossing experiments also place *C. ecuadorensis* in the secondary gene pool for pumpkin (Lira-Saade 1995). Finally, *C. argyrosperma, C. ficifolia, C. lundelliana* and *C. pepo* form the tertiary gene pool.

5.2.4 *Cucurbita moschata*

As discussed for cushaw, *C. argyrosperma* and *C. moschata* are sister species (Kates et al. 2017), and *C. argyrosperma* comprises the secondary gene pool for butternut squash (*C. moschata*). As defined by Lira-Saade (1995), the butternut squash tertiary gene pool is formed by *C. ficifolia, C. maxima* and *C. pepo*. However, the broad crossability of butternut squash within the genus may merit the addition of further congeneric taxa to its secondary and tertiary gene pools with further study. As with *C. lundelliana, C. moschata* may serve as a bridging species in interspecific crosses.

5.2.5 *Cucurbita pepo*

The primary gene pool of summer squash (*C. pepo*) includes three interfertile subspecies: *C. pepo* subsp. *fraterna, C. pepo* subsp. *ovifera* and *C. pepo* subsp. *pepo.* As in the case of *Cucumis melo*, summer squash experienced two independent domestication events, resulting in the two cultivated subspecies known today, subsp. *ovifera* and subsp. *pepo* (Paris et al. 2012). Note that no wild progenitor has yet been identified for subsp. *pepo*, but a wild form of subsp. *ovifera* occurs throughout southern USA (Chomicki et al. 2020). As discussed in Section 3.2, *C. pepo* subsp. *fraterna* is a wild form that naturally occurs in northeastern Mexico, but is not the wild progenitor of either domesticated subspecies (Kates et al. 2017). As with *C. argyrosperma* and *C. maxima*, the cultivated and wild forms of *C. pepo* occur in sympatry in parts of the range, and natural hybridization is a frequent occurrence (Merrick 1991).

Despite the high morphological and genetic variability seen in summer squash (Gong et al. 2013), the crop is particularly susceptible to viral diseases of the *Cucurbita* (Lebeda et al. 2007). However, attempts to obtain the necessary resistance alleles from wild species are limited by the poor crossability of *C. pepo* with other congeneric species, necessitating techniques such as embryo rescue. Nonetheless, some of the closest evolutionary relatives of summer squash occur in its secondary (*C. argyrosperma, C. ecuadorensis, C. moschata, C. okeechobeensis*) and tertiary (*C. ficifolia, C. lundelliana, C. maxima*) gene pools (Lira-Saade 1995).

5.2.6 Crop wild relatives

Of the CWRs of cultivated *Cucurbita* species, 11 taxa are found in Mexico; four of these are endemic. To illustrate the overlap among species distributions, and the potential for sympatry with the cultivated taxa, the distributions of the CWRs are shown in Figure 5.1.

5.3 *Citrullus*

As discussed in previous sections, the genus *Citrullus* contains one major crop, the sweet dessert watermelon (*C. lanatus*), as well as three minor crops: citron melon (*C. amarus*), colocynth (*C. colocynthis*) and egusi melon (*C. mucosospermus*). At present, three additional wild species are recognized within the genus: *C. ecirrhosus*, C. *naudinianus* and *C. rehmii.* All species in the genus share the same chromosome number (2n = 22) and are cross-compatible to varying degrees (Lebeda et al. 2007). For example, even crosses between *C. lanatus* and the more distantly related *C. colocynthis* (see phylogeny in Renner et al. 2019) may produce fertile hybrids (Bates and Robinson 1995). Among the *Citrullus* species, *C. colocynthis* has the highest genetic diversity (Levi et al. 2000), and may possess useful resistance to various insect pests. However, a comprehensive assessment of the genus, in terms of both useful agronomic traits and interspecific hybridization, remains lacking. The gene pools for dessert watermelon are still officially undefined. Though we might speculate that the six other *Citrullus* species form the secondary gene pool of dessert watermelon, the tertiary gene pool has not been characterized.
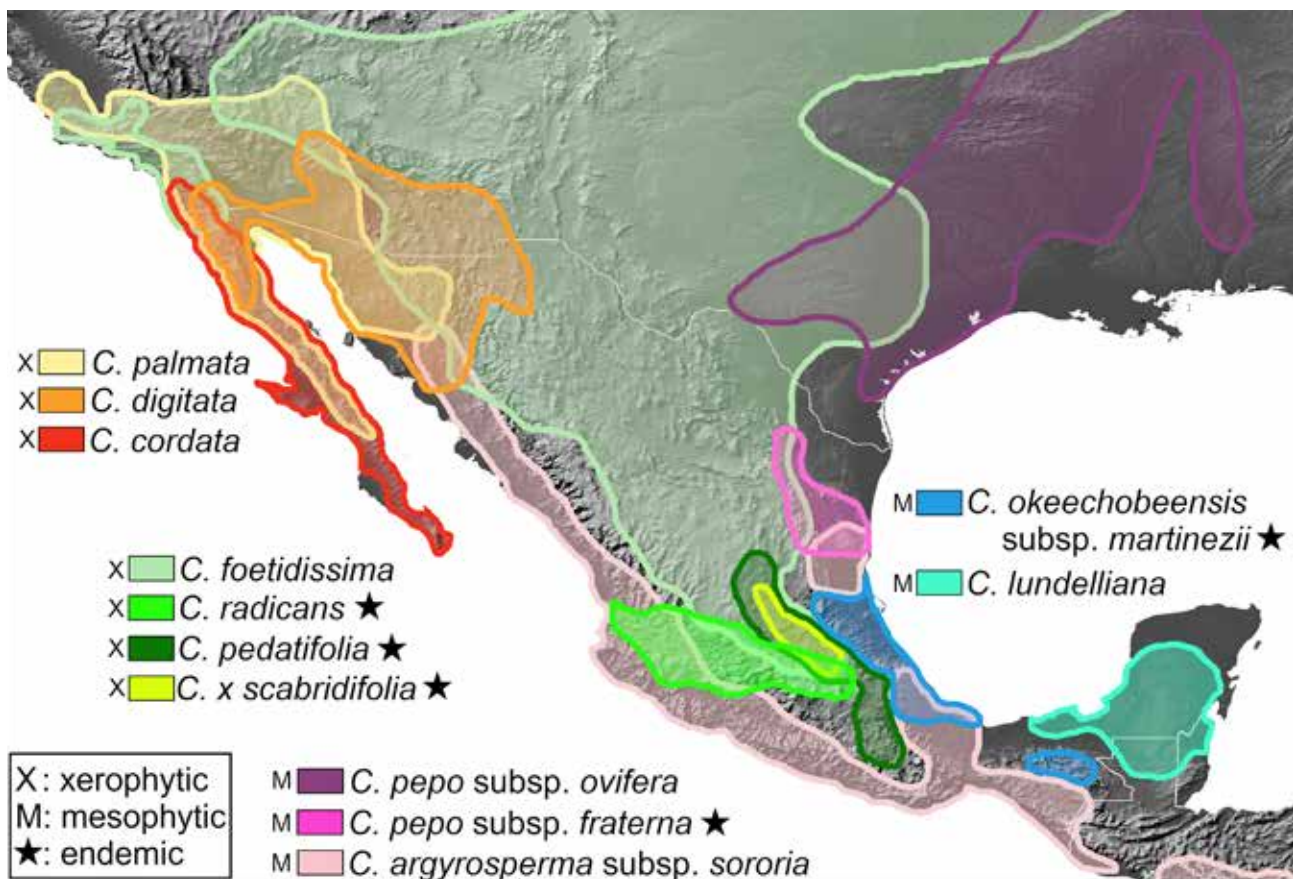
Figure 5.1 General distribution of wild Cucurbita from Mexico based on 1946 unique records of the Sistema Nacional de Información sobre Biodiversidad (SNIB Conabio), Lira (1995), Red de Herbarios del Noroeste de México and potential distributions of Castellanos-Morales et al. (2018). Original figure published in Aguirre-Dugua et al (2020).

Summer Squash. *Cucurbita pepo* (1857).
Source: Swallowtail Garden Seeds/Flickr

6 OVERVIEW OF *EX SITU* COLLECTIONS

6.1 *Cucumis*

According to the World Information and Early Warning System (WIEWS) of FAO, there are currently 28,093 *Cucumis* accessions conserved *ex situ* in 113 genebanks located in 66 countries around the globe (Table 6.1). The highest number of accessions and species (28) are held in Europe (49 genebanks located in 24 countries), followed by Asia, the center of origin and diversity of *Cucumis sativus* (cucumber) and most likely also *Cucumis melo* (muskmelon). In eastern Europe, 4,292 accessions are conserved, mostly in Bulgaria, Ukraine, Poland and the Czech Republic, the latter country conserving 15 different species. In southern Europe, 3,124 accessions are held, mostly by

Spain (2,702 accessions; 15 species). Western Europe conserves 2,340 accessions, held mainly by Germany (1,170 accessions; 18 species) and the Netherlands (1,004; two species). In East Asia, 5,116 accessions are held, mostly by Japan (4,684 accessions). South Asia conserves 3,464 *Cucumis* accessions, which are predominantly held in India (2,009 accessions; 20 species) and Bangladesh (1,279 accessions). The 6,372 accessions held in the Americas are mostly kept in North American genebanks (5,484 accessions; 18 species).

A small amount of *Cucumis* germplasm is held in regional genebanks (172 accessions): CATIE, Costa Rica (25); ICBA, United Arab Emirates (40); NordGen, Sweden (101); and the SADC Plant Genetic Resources

Table 6.1 *Cucumis* germplasm held *ex situ* by region and type of genebank (national, regional and international) as per the WIEWS database (consulted December 2019).

Region	Accessions	Species	Genebanks	Countries
Africa	1,885	19	16	16
Americas	6,372	19	18	11
Asia	9,117	22	23	15
Europe	9,885	28	49	24
Regional	172	4	4	–
International	662	2	3	–
TOTAL	**28,093**	**46**	**113**	**66**

Center (SPGRC; 6)). International genebanks are keeping 662 accessions, shared by ICARDA, Lebanon and Morocco (18); ILRI, Ethiopia (1); and WorldVeg genebank (643).

According to WIEWS, 39% of the *Cucumis* accessions conserved in 113 genebanks located in 66 countries are landraces or traditional cultivars. However, a significantly large proportion (28%) of *Cucumis* accessions are of unknown biological status; other accessions are breeding/research material (17%), wild species (9%) and advanced cultivars (8%). The large proportion of collections with unknown biological status is a major issue confounding the interpretation of the composition of published/reported *ex situ* Cucurbitaceae germplasm holdings around the globe.

The numbers of accessions conserved per *Cucumis* species, according to the data available in WIEWS, Genesys and the USDA-GRIN databases, are listed in Appendix IX. The same dataset, along with data from the strategy survey, was used to determine the number of *Cucumis* accessions conserved *ex situ* by each holding institute (Appendix X).

Cucumis melo has the highest number of accessions conserved *ex situ*, followed by *C. sativus* (Appendix IX). *Cucumis anguria* and *C. metuliferus* have a more limited geographic range of cultivation, which is reflected in the relatively low number of accessions conserved *ex situ*. The proportion of accessions with unidentified *Cucumis* taxa accounts for about 3% of the combined dataset (WIEWS, Genesys, USDA-GRIN). Species identification should be resolved during regeneration events.

The major holding institutes of *C. dipsaceus* are DEU146, IPK, Germany; ESP058, CSICELM, Malaga, Spain; KEN212, GeRRI, Kenya; and CZE122, CRI, Czech Republic. Most accessions of *C. africanus* are held by BWA015, NPGRC, Botswana; DEU146; IND001, NBPGR, India; KEN212; GBR004, Millennium Seedbank, Kew, Great Britain; USA020, NC7, Ames, Iowa, USA; and CZE122. *Cucumis myriocarpus* is conserved by BGR001,

IPGR, Bulgaria; DEU146; IND001; KEN212; GBR004; USA020; and CZE122. The major holding institutes of *C. prophetarum* are IND001; KEN212; and GBR004. *Cucumis trigonus* and *C. sativus* var. *hardwickii* are mostly conserved by IND001.

A search of the WIEWS database in May 2011 and March 2016 revealed a total of 44,298 and 44,402 *Cucumis* accessions, respectively (Ebert 2013; Ebert 2019), a significant difference of 5,175 and 5,279 accessions, respectively, compared to current holdings (WIEWS database results, plus data from genebanks currently not reporting in WIEWS that were obtained through the strategy survey). This difference can be explained by the fact that countries with large collections are not yet, or not yet fully, reporting accession-level data for 2018. These gaps in the data are an indication that we are still far from a robust and reliable global germplasm reporting system.

6.2 *Cucurbita*

According to the WIEWS database, there are currently 28,412 *Cucurbita* accessions held *ex situ* in 118 genebanks and 65 countries. A large proportion of these (11,927 accessions) are conserved in the Americas, the center of origin and diversity of most of the *Cucurbita* taxa (Table 6.2). About 58% of the germplasm conserved in the Americas is found in South America (6,908 accessions), including four genebanks in Brazil, which is a major holder of *Cucurbita* germplasm (5,832 accessions; 10 species). Most genebanks are centralized within a country, with possible duplications at other sites. Brazil has instituted a regional system as a rational way to deal with very broad genetic diversity in a large country. This has the advantage that most accessions can be regenerated in an environment similar to that of the original site of the collection.

There are four regional genebanks that conserve *Cucurbita* germplasm: CATIE, Costa Rica (2,119 accessions); ICBA, United Arab Emirates (50); NordGen, Sweden (6); and the SADC Plant Genetic Resources Center (SPGRC; 262). Furthermore, two international

Table 6.2 *Cucurbita* germplasm held *ex situ* by region and type of genebank (national, regional and international) as per WIEWS database (consulted December 2019).

Region	Accessions	Species	Genebanks	Countries
Africa	3,041	6	16	16
Americas	11,927	19	31	14
Asia	2,166	8	20	14
Europe	7,720	17	45	21
Regional	2,437	7	4	–
International	1,121	5	2	–
TOTAL	**28,412**	**24**	**118**	**65**

genebanks (ICARDA, Lebanon and Morocco (6 accessions) and WorldVeg, Taiwan (1,115)) also conserve *Cucurbita* germplasm.

Genebank curators often choose to conserve some combination of local and introduced landraces, advanced/improved cultivars, breeding or other experimental materials, and CWRs. Approaches vary widely in terms of emphasis on these different categories. Local landraces are often the nucleus of most collections and comprise most accessions of a given genus. According to WIEWS, 48% of the *Cucurbita* germplasm conserved in 118 genebanks around the globe are landraces or traditional cultivars. However, a similarly large proportion (40.4%) of the *Cucurbita* collections are of unknown biological status, with advanced/improved cultivars, breeding/research material and CWRs accounting for about 11% of the total holdings. The large proportion of collections with unknown biological status is a major issue confounding the interpretation of the published/reported *ex situ* Cucurbitaceae germplasm holdings around the globe.

Cucurbita moschata has the highest number of accessions conserved *ex situ*, followed by *C. pepo* and *C. maxima* (Appendix XI). About 15% of accessions in the combined WIEWS-Genesys-USDA-GRIN dataset are not identified to species. Species identification may be resolved during regeneration events. A small number of institutes conserve the bulk of the CWRs (see Table 6.3). *Cucurbita pepo* var. *ovifera* is mainly conserved at ARM059 (72), UKR021 (11) and UKR048 (10).

Major holding institutes of *Cucurbita* accessions conserved *ex situ* are listed in Appendix XII; data were

collated from the WIEWS, Genesys and USDA-GRIN databases, and from the strategy survey. Searches of the WIEWS database in May 2011 and March 2016 revealed a total of 39,583 and 40,055 *Cucurbita* accessions, respectively (Ebert 2013; Ebert 2019), a significantly higher number of accessions (difference of 8,417 and 8,889, respectively) compared to current holdings (WIEWS database results plus data from genebanks currently not reporting in WIEWS that were obtained through the strategy survey).

It is difficult to explain these differences as there was an increase in *Cucurbita* holdings reported in WIEWS from 2011 to 2016, and then a dramatic loss of close to 9,000 accessions during the three years after that. Moreover, significantly lower figures were reported in the 2019 online survey by the VIR genebank (RUS001; 2,992 accessions) and CAAS (CHN001; 1,420) compared to March 2016 data reported in WIEWS of 5,771 and 1,767 accessions, respectively. The cause of these discrepancies is not clear.

6.3 *Citrullus*

Although the genus *Citrullus* originated primarily in Africa, most accessions held *ex situ*, according to the WIEWS database, are found in the Americas and in Europe (Table 6.4). Overall, 9,169 *Citrullus* accessions are held *ex situ* in 81 genebanks in 49 countries. Most of the accessions conserved in the Americas are held in North America (1,930), followed by South America (1,394), almost exclusively by Brazil (1,360 accessions). More than 50% of the *Citrullus* germplasm held in European genebanks is kept in eastern Europe (1,144 accessions), and most of the southern European acces-

Table 6.3 Number of accessions of each *Cucurbita* crop wild relative conserved in six genebanks. Based on data from Genesys (December 2020), WIEWS (December 2020) and USDA-GRIN (March 2020)

Taxa	BRA003	USA020	USA016	CZE122	JPN183	MEX208
Cucurbita argyrosperma subsp. *sororia* (L.H. Bailey) L. Merrick & D.M. Bates	25	0	62	22	0	1
Cucurbita digitata A. Gray	0	0	20	0	0	1
Cucurbita ecuadorensis H.C. Cutler & Whitaker	3	0	9	1	0	0
Cucurbita foetidissima Kunth	28	0	3	5	19	19
Cucurbita lundelliana L.H. Bailey	11	0	20	0	0	1
Cucurbita maxima subsp. *andreana* (Naudin) Filov	0	0	0	0	0	0
Cucurbita okeechobeensis subsp. *martinezii* (L.H. Bailey) T.C. Andres & Nabhan ex T.W. Walters & D.S. Decker	8	0	26	7	0	0
Cucurbita palmata S. Watson	0	0	31	0	0	0
Cucurbita pedatifolia L.H. Bailey	0	0	3	0	0	2
Cucurbita pepo subsp. *fraterna* (L.H. Bailey) Lira et al.	4	4	0	4	0	0
Cucurbita pepo subsp. *ovifera* (L.) D.S. Decker	0	1	0	26	0	0
Cucurbita pepo var. *ovifera* (L.) Harz	3	0	0	0	0	0
Cucurbita pepo var. *ozarkana* D.S. Decker	0	43	0	0	0	0
Cucurbita pepo var. *texana* (Scheele) Filov	24	14	0	0	0	0
Cucurbita radicans Naudin	0	0	4	0	0	0

sions (614) are conserved in Spain (465 accessions). The Asian *Citrullus* germplasm is shared between East Asia (995 accessions; Japan: 795; Mongolia: 200), South Asia (542 accessions; India: 450; Pakistan: 90) and West Asia (266). The 1,720 African *Citrullus* accessions are shared between Southern Africa (796; South Africa: 515; Botswana: 184), North Africa (525; Sudan: 471) and East Africa (399; Tanzania: 149; Zambia: 114; Malawi: 111).

There are three regional genebanks that conserve a total of 179 *Citrullus* accessions (the SADC Plant Genetic Resources Center (SPGRC, ZMB030; 136); ICBA, United Arab Emirates (34); CATIE, Costa Rica (9), and three international genebanks conserving a total of 63 accessions (WorldVeg, Taiwan (57); ICARDA, Lebanon and Morocco (4); and ILRI, Ethiopia (2)).

According to WIEWS, 37.4% of the *Citrullus* germplasm conserved in 81 genebanks are landraces or traditional cultivars, 8.8% wild species, 7.7% breeding/research materials and 6.1% improved cultivars (Table 6.5). However, almost 40% of accessions conserved are of unknown biological status. This large proportion of *Citrullus* collections with unknown biological status is a major issue when trying to assess the value of collections for breeding or other purposes. It is urgent to clarify the biological status of this large proportion

of *Citrullus* accessions during regeneration or characterization activities.

Holding institutes of *Citrullus* accessions conserved *ex situ* are listed in Appendix XIII; data were collated from WIEWS, Genesys and USDA-GRIN, as well as the strategy survey.

Searches of the WIEWS database in May 2011 and March 2016 revealed a total of 15,143 and 15,144 *Citrullus* accessions, respectively (Ebert 2013; Ebert 2019), a modestly higher number of accessions (difference of 934) compared to current holdings (WIEWS database results plus data from genebanks currently not reporting in WIEWS that were obtained through the strategy survey). UzRIPI (UZB006) and CAAS (CHN001) reported a substantially higher number of *Citrullus* accessions in 2011 and 2016 compared to the recent online survey, but this was compensated by a substantially higher number of accessions reported by the VIR genebank (RUS001) in the online survey compared to the WIEWS 2011 and 2016 data. The main difference between the 2011 and 2016 data and the current results is due to the absence of the national genebank of Israel (ISR002) in the current reports, as this institute reported 840 *Citrullus* accessions in 2011 and 2016.

Table 6.4 *Citrullus* germplasm held *ex situ* by region and type of genebank (national, regional and international) as per WIEWS database, consulted December 2019.

Region	Accessions	Species	Genebanks	Countries
Africa	1,720	5	12	12
Americas	3,333	4	14	10
Asia	1,804	3	19	13
Europe	2,070	6	30	14
Regional	179	2	3	–
International	63	2	3	–
TOTAL	**9,169**	**7**	**81**	**49**

Table 6.5 *Citrullus* taxa and corresponding number of accessions[1] conserved globally based on data from Genesys (February 2020), WIEWS (February 2020) and USDA-GRIN (March 2020).

Taxon	Biological status	Accessions
Citrullus lanatus (Thunb.) Matsum. & Nakai	Cultivated, wild	8,403
Citrullus colocynthis (L.) Schrad.	Wild (and sparingly cultivated)	313
Citrullus sp.	Cultivated, wild	253
Citrullus amarus Schrad.	Wild, cultivated	227
Citrullus mucosospermus (Fursa) Fursa	Cultivated	50
Citrullus ecirrhosus Cogn.	Wild	9
Citrullus rehmii De Winter	Wild	7
Citrullus naudinianus (Sond.) Hook. f.	Wild	2
TOTAL	**Cultivated, wild**	**9,264**

[1]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

6.4 Luffa

According to the WIEWS and Genesys databases, 3,279 *Luffa* accessions are currently being conserved *ex situ*, at the global level (Table 6.6). The largest holder of *Luffa* germplasm is the international WorldVeg genebank (TWN001, 871 accessions), followed by national genebanks in India (IND001; 708); Bangladesh (BGD206, Lal Teer Seed Ltd (478); BGD003, BARI (355); USA (USA016, S9, Griffin, Georgia; 167); Brazil (BRA003, CENARGEN; 144), Japan (JPN183, NARO; 134); and Pakistan (PAK001, PGRP; 119). Global germplasm holders, based on WIEWS, Genesys and USDA-GRIN databases, as well as data from the strategy survey, are listed in Appendix XIV.

According to the databases accessed, *L. aegyptiaca* has the highest number of *ex situ* accessions, followed by *L. acutangula* (Table 6.6). In the combined dataset, 5.6% of species are unidentified. Accessions of wild taxa are rather limited and *L. astorii* is not represented at all in *ex situ* collections. *Luffa operculata* was considered a synonym of *L. sepium* following Filipowicz et al. (2014).

6.5 Benincasa

At the global level, 1,650 *Benincasa* accessions are currently being conserved *ex situ*, according to the WIEWS and Genesys databases, as well as data taken from the strategy survey for the VIR genebank in Russia and CAAS in China (Appendix XV). The largest holder of *Benincasa* germplasm is the international WorldVeg genebank (TWN001, 315 accessions), followed by national genebanks in China (CHN001, 300), India (IND001, 270), Japan (JPN183, 261) and Bangladesh (BGD206, 172; BGD003, 151).

Analysis of the data from Genesys, WIEWS and USDA-GRIN databases revealed that *B. hispida* has the highest number of *ex situ* accessions (1,258), followed by *B. fistulosa* (31) (Table 6.7). In the combined dataset, about 2% of species are unidentified.

6.6 Lagenaria

In total, 5,731 *Lagenaria* accessions are currently being conserved *ex situ* globally, according to data collated from WIEWS, Genesys and USDA-GRIN, as well as from the strategy survey (Appendix XVI). The largest holders of *Lagenaria* germplasm are located mainly, but not exclusively, in Asia and Africa: the national genebanks of India (IND001; 743), Kenya (KEN012; 478), the USA (USA016; 900), China (CHN001; 370), South Africa (ZAF062; 350), Japan (JPN183; 174) and Bangladesh (BGD206; 345), and the international WorldVeg genebank (TWN001; 346).

The number of accessions conserved globally for each *Lagenaria* species is shown in Table 6.8.

Table 6.6 *Luffa* taxa and corresponding number of accessions[1] conserved globally, based on Genesys, WIEWS and USDA-GRIN (February 2020).

Taxon	Biological status	Accessions
Luffa aegyptiaca Mill. (*L. cylindrica*)	Cultivated (mostly), wild	1,610
Luffa acutangula (L.) Roxb.	Cultivated	1,400
Luffa sp.	Cultivated, wild	184
Luffa acutangula var. *amara* (Roxb.) C.B. Clarke	Wild form of *Luffa acutangula*	69
Luffa echinata Roxb.	Wild	6
Luffa graveolens Roxb.	Wild	5
Luffa sepium (G. Mey.) C. Jeffrey	Wild	4
Luffa saccata F. Muell. ex Naudin	Wild	1
TOTAL	**Cultivated, Wild**	**3,279**

[1]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

Table 6.7 *Benincasa* taxa and corresponding number of accessions conserved globally, based on Genesys, WIEWS and USDA-GRIN (February 2020).

Taxon	Biological status	Accessions
Benincasa hispida (Thunb.) Cogn.	Cultivated	1,258
Benincasa fistulosa (Stocks) H. Schaef. & S.S. Renner	Cultivated	31
Benincasa sp.	Cultivated	31
TOTAL	**Cultivated**	**1,320**

6.7 Momordica

In total, 3,026 *Momordica* accessions are currently being conserved *ex situ* globally, according to data collated from the WIEWS, Genesys and USDA-GRIN databases, and from the strategy survey (Appendix XVII). The largest holders of *Momordica* germplasm are located in Asia, where commercial production of *Momordica* species is concentrated. The largest collection (814 accessions) is held by Lal Teer Seed Ltd. (BGD026) in Bangladesh, followed by the international WorldVeg genebank (TWN001, 622), the national genebank of India (IND001; 584) and the national genebanks of Japan (JPN183; 383) and China (CHN001; 200).

According to data from WIEWS, Genesys and USDA-GRIN databases, *Momordica charantia* has by far the highest number of accessions (2,342) conserved *ex situ* (Table 6.9). *Momordica angustisepala*, *M. boivinii*, *M. cabrae*, *M. calantha*, *M. charantia* subsp. *macroloba*, *M. cissoides* and *M. subangulata* subsp. *subangulata* are not at all represented in *ex situ* collections. In the Genesys and WIEWS databases, 9.6% and 10.2% of species are unidentified, respectively.

6.8 Taxa standardization

Information on the taxa standardization conducted in order to compile and analyze accession records from Genesys, WIEWS and USDA-GRIN is given in Appendix XVIII.

Table 6.8 *Lagenaria* taxa and corresponding number of accessions[1] conserved globally, based on data from Genesys, WIEWS and USDA-GRIN (February 2020).

Taxon	Biological status	Accessions
Lagenaria siceraria (Molina) Standl.	Cultivated, wild	4,445
Lagenaria spp.	Wild	497
Lagenaria sphaerica (Sond.) Naudin	Wild	124
Lagenaria abyssinica (Hook. f.) C. Jeffrey	Wild	20
Lagenaria breviflora (Benth.) Roberty	Wild	9
TOTAL	**Cultivated, Wild**	**5,095**

[1]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

Table 6.9 *Momordica* taxa and corresponding number of accessions[1] conserved globally, based on data from Genesys, WIEWS and GRIN-USDA (February 2020).

Taxon	Biological status	Accessions
Momordica charantia L.	Cultivated (mostly), wild	2,342
Momordica sp.	Cultivated, wild	84
Momordica balsamina L.	Cultivated, wild	78
Momordica dioica Roxb. ex Willd.	Cultivated	54
Momordica cochinchinensis (Lour.) Spreng.	Cultivated, wild	13
Momordica subangulata subsp. renigera (Wall. ex G. Don) W.J. de Wilde	Cultivated, wild	12
Momordica cardiospermoides Klotzsch	Cultivated, wild	9
Momordica foetida Schumach.	Wild	8
Momordica sahyadrica Kattuk. & V.T. Antony	Wild	8
Momordica rostrata A. Zimm.	Wild	6
Momordica trifoliolata Hook. f.	Wild	5
Momordica involucrata E. Mey.	Cultivated	4
Momordica spinosa Chiov.	Wild	3
Momordica cymbalaria Hook. f.	Wild	2
Momordica peteri A. Zimm.	Cultivated, wild	2
Momordica anigosantha Hook. f.	Wild	1
Momordica repens Bremek.	Wild	1
Momordica subangulata Blume	Wild	1
TOTAL	Cultivated, wild	**2,633**

[1]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

7 COLLECTION GAPS

7.1 The Cucurbitaceae diversity tree

Diversity trees for *Cucurbita* and *Cucumis* crops were generated as part of the development of this strategy. A diversity tree is a representation of the overall structure of crop diversity obtained by dividing the diversity within a crop gene pool in a hierarchical manner. The structure of the tree is based on published information and consultation with experts. The original idea of diversity trees was proposed in a paper by Van Treuren et al. (2009).

An interactive version of the diversity trees for *Cucurbita* and for *Cucumis* crops can be found in Genesys. Gaps in the *ex situ* collections of *Cucurbita*, *Cucumis* and *Citrullus* crops were assessed by analyzing a dataset that combined the passport data available in Genesys, WIEWS and GRIN-USDA in February 2020. (Note that at the time of analysis, WIEWS 2018 was available; however, later in 2020, FAO uploaded the WIEWS 2019 dataset). This dataset was analyzed to look at the coverage, in terms of number of accessions, of the groups in the diversity trees for *Cucurbita* and *Cucumis*.

7.2 Composition and gaps in *ex situ* collections

It has been highlighted that native diversity of several cucurbit species still needs to be explored and collected on a priority basis (Pessarakli 2016). According to the Cucurbitaceae strategy survey, 68% of genebanks (17 out of 25 respondents) feel that species coverage of the cucurbit crops conserved *ex situ* is insufficient; 56% of respondents highlighted insufficient ecological representation of the species conserved and 44% noted that population (sample) representation per species is deficient (Table 7.1). Asked about plans to fill the mentioned gaps, 45.45% of respondents reported having plans to fill the gaps, 18.18% were not sure and 36.36% said there were no plans to fill the gaps.

During the strategy consultation workshop, experts noted the following:
- Filling collection gaps as soon as possible is most important.
- It is important to fill collections gaps for wild relatives in the Americas and for landraces in primary

Table 7.1 Major gaps in *ex situ* collections, as identified by survey respondents.

	Are there major collection gaps?			
	Yes	**No**	**Don't know**	**Total**
Species coverage of the crop	68%	24%	8%	100%
	17	6	2	25
Population (sample) representation per species	44%	36%	20%	100%
	11	9	5	25
Ecological representation of the species	56%	24%	20%	100%
	14	6	5	25

regions of diversity (e.g., Mexico) as well as other regions with interesting landrace diversity (e.g., Myanmar, China).

- In Mexico, there is landrace diversity in *C. moschata* along an altitude gradient (highlands versus lowlands). *C. moschata* genetic diversity could also be found in Colombia and Brazil.
- Collecting of *C. pepo* has been neglected in northern Mexico.
- It is important to prioritize collecting in extreme environments to capture abiotic stress tolerance and in areas with high pest and disease resistance to identify genotypes presenting single or multiple resistance.
- More sources of resistance to diseases and insect pests are needed for cucurbit crops. There is also a high demand for stress tolerance against heat, cold, drought, salt and acidity. Ideally, abiotic and biotic stress tolerance should be combined.
- A major focus of collecting should be on CWR, since habitats are changing so rapidly due to climate change, and landraces of "minor" crops should be a focus of collecting.
- Collaboration with national genebanks, universities or other stakeholders willing to collect and move seeds across borders (after appropriate permits, collecting agreements and phytosanitary certificates have been secured) should be encouraged and strengthened.
- Genebank collectors often go back to the same areas where germplasm was previously collected. There is a need to explore more geographically isolated areas where no collecting has been done before.
- Some important collections are held by universities and private individuals, or organizations, that are not yet reflected in national, regional or international collections or international databases such as Genesys and WIEWS. Therefore, connectivity with universities and other collections should be enhanced with the aim of registering all existing diversity and capture diverse and novel germplasm and make it available to users. Such efforts need to start at the national level where breeders and other research staff are aware of the existence of such collections.

In the following sections, we discuss potential diversity gaps for each genus based on the following information: the number of accessions in the end groups of the corresponding diversity trees (for *Cucurbita* and *Cucumis* crops), information published in research papers and

expert opinion recorded during the consultations conducted as part of developing this strategy.

7.2.1 *Cucurbita*

CWRs

For CWRs of *Cucurbita*, the recent publication by Khoury et al. (2020) is a major resource highlighting collecting gaps for each species (Figure 7.1). Based on the modeled distribution area and the area covered by current collections, they found that *C. cordata*, *C. pedatifolia*, *C. radicans* and *C. x scabridifolia* are high priority for further collecting, followed by *C. foetidissima*, *C. digitata* and *C. palmata*. Overall, these findings are consistent with the low number of accessions conserved *ex situ* found in the analysis conducted for this strategy. The maps of the modeled distributions and of the gaps of *Cucurbita* wild species are freely available in the supporting information of Khoury et al. (2020).

The genetic diversity of wild *Cucurbita* species in the USA is decreasing due to habitat loss, and the cultivation of genetically modified squashes (e.g., virus-resistant *Cucurbita pepo*) in Mexico and the USA is also a potential threat to wild *C. pepo* populations, owing to the high risk of hybridization. The wild relatives of pumpkin are also limited in their dispersion because the original megafauna disperser became extinct fol-
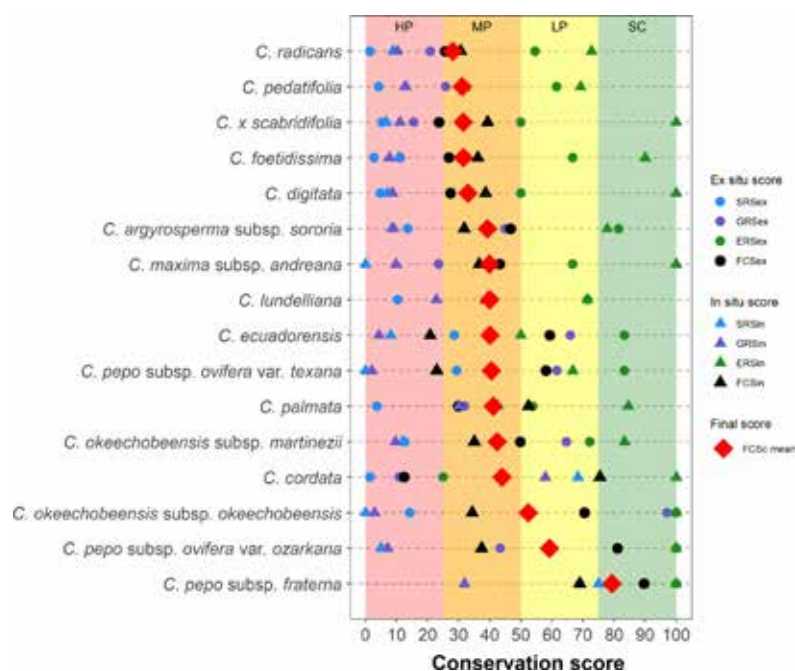
Figure 7.1 Results of the conservation gap analysis for each taxon of wild *Cucurbita*. HP: High Priority, MP: Medium Priority, LP: Low Priority, SC: Sufficiently Conserved; SRSex: sampling representativeness score *ex situ*, GRSex: geographic representativeness score *ex situ*; ERSex: ecological representativeness score *ex situ* for *ex situ*; SRSin: sampling representativeness score *in situ*; GRSin: geographic representativeness score *in situ*; ERSin: ecological representativeness score *in situ*. Source: Khoury et al. (2020)

lowing the arrival of humans on the American continent (Kistler et al. 2015).

For each wild *Cucurbita* taxon, the numbers of accessions conserved *ex situ*, based on data from Genesys, WIEWS and USDA-GRIN, are listed in Table 6.3 and Appendix XI.

Among the CWRs, *Cucurbita radicans* has been assessed as globally endangered, while *C. okeechobeensis* subsp. *okeechobeensis* is nearly extinct; other *Cucurbita* wild relatives are rare. *Ex situ* collections of *Cucurbita* germplasm in Mexico, a major center of origin and diversity for the genus, are severely threatened and rapidly losing viability.

Landraces and cultivars

Cucurbita argyrosperma subsp. *argyrosperma*

We found 48 accessions of this crop from Mexico, 10 from the USA, one from Guatemala and one from Argentina. Larger numbers of accessions are conserved at INIFAP (302) and SINAREFI (164) in Mexico, but these collections are at risk (Xitlali Aguirre-Dugua, personal communication, expert consultation workshop Thailand, 11-13 Dec. 2019). This suggests that further collecting of landraces in Central America and duplication of collections at risk should be a priority.

Cucurbita moschata

Hernández-Rosales et al. (2020) found two patterns of genetic differentiation in Mexican landraces: one pattern according to an elevation gradient differentiating between lowland and highland landraces (>1200 m) and a geographic pattern with two main clusters (Continental Mexico and Yucatan Peninsula).

In the data from Genesys, WIEWS and USDA-GRIN, we found 193 landraces collected in Mexico (conserved in USA016 and CRI001), but this is an underestimate because these data did not include *C. moschata* conserved in Mexican institutes. A total of 261 accessions of *C. moschata* are maintained at INIFAP and SINAREFI (Xitlali Aguirre-Dugua, personal communication, expert consultation workshop Thailand, 11-13 Dec. 2019); however, these are at risk due to the seed storage conditions.

A distribution plot for elevation of the landraces collected in Mexico (Figure 7.2) shows that highland landraces are less represented in *ex situ* collections. Figures 7.3 and 7.4 show the collection sites for accessions where coordinate data are available. In the Americas, the highest numbers of accessions came from Guatemala (694), Costa Rica (512), Brazil, Mexico (193) and Honduras (137) (Table 7.2).

Figure 7.3 Collecting sites (orange points) in the Americas for landraces of *C. moschata*, as recorded in Genesys, WIEWS and USDA-GRIN. Only accessions with coordinate data are shown.

Figure 7.2 Distribution and rug plot for the elevation of landraces of *C. moschata* collected in Mexico. Elevation in meters is on the x-axis. Number of accessions is on the y-axis.

Figure 7.4 Collecting sites (orange points) in Africa, Europe and Asia for landraces of *C. moschata*, as recorded in Genesys, WIEWS and USDA-GRIN. Only accessions with coordinate data are shown.

In Europe, a sizable proportion of accessions were collected in Spain (302) and Portugal (132) (see Table 7.2). In our dataset, we found 304 landraces of *C. moschata* collected in Africa, mostly in Zambia (124), Zimbabwe (101) and Kenya (70). Of the 169 landraces of *C. moschata* from Asian countries, 47 are from Thailand and 36 are from Bangladesh. No accessions of landraces from Myanmar are recorded in our dataset, although it has been suggested that Myanmar has interesting diversity (personal observation, strategy expert consultation workshop, Thailand, 11–13 Dec. 2019). Japan is considered a secondary center of diversity for *C. moschata* (Esquinas-Alcazar and Gulick 1983), but there are no accessions of landraces of this species from Japan in our dataset (but there are some with unknown biological status). However, our dataset does not include accessions conserved at NARO (JPN003/JPN183); the NARO database, accessible on the web (NARO 2020), lists 17 accessions of landraces from Japan. These figures suggest that the primary center of diversity of *C. moschata* (Mexico, Central America and northern South America) is better represented *ex situ* than secondary centers of diversity. This is consistent with the greater genetic diversity expected in this area for this crop. However, only 15 accessions come from Colombia, where great diversity has also been observed (Zhiteneva 1930).

Cucurbita ficifolia

Table 7.3 shows the origin of landraces of *C. ficifolia* conserved *ex situ* in the data from Genesys, WIEWS and USDA-GRIN. This dataset includes no records of accessions from Asia, where it is a popular crop (Nee 1990).

Cucurbita maxima

In our dataset from Genesys, WIEWS and USDA-GRIN, the number of accessions of landraces from South America, and in particular from Brazil, Argentina, Chile and Bolivia (the primary center of diversity), is relatively low (Table 7.4). Similarly, Asia (in particular, India, Bangladesh and Myanmar), its secondary center of diversity, is not well represented. As only 43% of the accessions of *C. maxima* in this dataset have known biological status, it is possible that these figures underestimate the number of landraces of *C. maxima* conserved *ex situ*. For example, there are 1,243 accessions of this taxa from Brazil, but these are mostly without record of biological status. In addition, in a more recent data upload into WIEWS, the Banco Activo de Germoplasma La Consulta (ARG1350) reported 86 accessions of landraces from Argentina, Instituto Nacional de Innovación Agropecuaria y Forestal of Bolivia (BOL317) reported 160 accessions of landraces from Bolivia, and Bangladesh Agricultural Research Institute (BGD003) reported 59 accessions of landraces from Bangladesh.

Table 7.2 Origin of landraces of *C. moschata* conserved *ex situ*, according to data from Genesys, WIEWS and USDA-GRIN. Countries with fewer than 20 accessions are not included in the table.

Country of origin	Accessions	Country of origin	Accessions
Guatemala	694	Zimbabwe	101
Costa Rica	514	Panama	75
Bangladesh	465	Peru	74
Mexico	423	Kenya	70
Brazil	304	Pakistan	52
Spain	302	Thailand	50
Unknown	266	El Salvador	37
Bolivia	182	Cuba	37
Zambia	139	Bulgaria	31
Honduras	137	Nicaragua	30
Portugal	132	Cambodia	26

Table 7.3 Origin of landraces of *C. ficifolia* conserved *ex situ*, according to data from Genesys, WIEWS and USDA-GRIN.

Country of origin	Accessions	Country of origin	Accessions
Mexico	113	Kenya	2
Guatemala	108	Romania	2
Spain	82	Hungary	2
Portugal	52	Honduras	1
Costa Rica	44	Colombia	1
Peru	43	Cuba	1
Bolivia	24	USA	1
Ecuador	14	El Salvador	1
Argentina	6	Unknown	1

Table 7.4 Origin of landraces of *C. maxima* conserved *ex situ*, according to data from Genesys, WIEWS and USDA-GRIN. Countries with fewer than 20 accessions are not included in the table.

Country of origin	Accessions	Country of origin	Accessions
Spain	409	Georgia	47
Zambia	405	Ukraine	44
Hungary	200	Mexico	42
Portugal	197	Unknown	39
Malawi	196	Pakistan	36
Tanzania	194	Tunisia	32
Poland	73	Lithuania	29
Romania	62	Uganda	27
Italy	62	Peru	27
Jordan	58	Zimbabwe	24
BGR	54	Bolivia	20

Cucurbita pepo subsp. *pepo*

A high number of the accessions of landraces of *Cucurbita pepo* subsp. *pepo* (Table 7.5) included in Genesys, WIEWS, and USDA-GRIN come from Mexico (Figure 7.5), the primary center of diversity, and a sizeable number of accessions come from its secondary center of diversity, namely Turkey and other Mediterranean countries.

7.2.2 *Citrullus*

The US National Plant Germplasm System holds a large collection of three *Citrullus* species, *C. lanatus*, *C. mucosospermus* and *C. amarus,* collected all over the world. Wild taxa in Africa, the center of origin and diversity for *Citrullus*, are not well represented in *ex situ* collections. *Citrullus ecirrhosus* and *C. rehmii* are recorded in the Genesys and WIEWS databases, but with fewer than 10 accessions each; there are only two accessions of *C. naudinianus* in *ex situ* collections. According to the recommendations of the *Citrullus* working group during the strategy workshop, North Africa, West Africa, Central and East Africa and South America should be targeted for additional collecting. Origin of landraces of *Citrullus lanatus* conserved *ex situ* are shown in Table 7.6.

7.2.3 *Cucumis sativus*

CWRs

In India, *Cucumis sativus* var. *hardwickii* is found in the foothills of the northwest Himalayas, Western and Eastern Ghats, Chota Nagpur Plateau and Central Plateau (Bisht et al. 2004) and in Thailand (Chomicki et al. 2020). Coordinate data are available for only 57 of the 174 accessions in our dataset (Genesys, WIEWS and USDA-GRIN). Figure 7.6 shows where these accessions were collected. No accessions in our dataset were collected in Thailand.

Cucumis hystrix, a CWR in the secondary gene pool of *C. sativus*, is found in South and Southeast Asia (southern China, Thailand, Bangladesh, Myanmar and northeast India) (Joseph John et al. 2018). According to the data in Genesys, WIEWS and USDA-GRIN, nine accessions of this taxa are conserved *ex situ*. Of these, six were collected in Laos (conserved at JPN183) and two in India (conserved at IND001); the other one has no record of origin. Lebeda et al. (2007) also include Myanmar, China and Thailand in its distribution, but according to our data, no accessions from these countries are conserved *ex situ*.

Landraces and cultivars

Lv et al. (2012) found that accessions from East Asia

Table 7.5 Origin of landraces of *C. pepo* conserved *ex situ*, according to data from Genesys, WIEWS and USDA-GRIN. Countries with fewer than 20 accessions are not included in the table.

Country of origin	Accessions	Country of origin	Accessions
Mexico	699	Bolivia	75
Spain	641	Pakistan	61
Portugal	381	Syria	47
Romania	370	Iran	43
South Africa	322	Lithuania	42
Hungary	266	Unknown	36
BGR	254	Ethiopia	35
Turkey	237	Argentina	32
Poland	211	Costa Rica	29
North Macedonia	123	Egypt	26
Guatemala	105	Peru	25
Italy	100	Albania	25
Ukraine	92	Croatia	20
Georgia	87		

Figure 7.5 Collecting sites (orange points) in Mexico for landraces of *C. pepo* subsp. *pepo*, as recorded in Genesys, WIEWS and USDA-GRIN. Only accessions with coordinate data are shown.
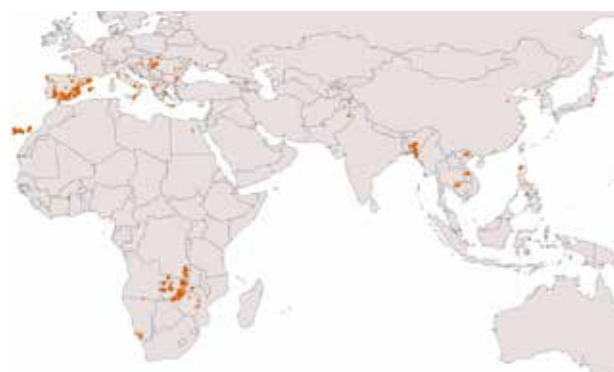
Table 7.6 Origin of landraces of *Citrullus lanatus* conserved *ex situ*, according to data from Genesys, WIEWS and USDA-GRIN. Countries with fewer than 20 accessions are not included in the table.

Country of origin	Accessions	Country of origin	Accessions
South Africa	468	Portugal	63
Spain	456	Mongolia	62
Sudan	430	Turkey	58
Botswana	218	China	40
Zambia	161	Ukraine	38
Unknown	156	Tunisia	35
Hungary	119	Italy	29
Bulgaria	112	Egypt	28
Malawi	110	Syria	24
Namibia	102	Turkmenistan	23
Zimbabwe	96	Albania	23
Pakistan	95	Bolivia	22

Figure 7.6 Sites where accessions of *Cucumis sativus* var. *hardwickii* were collected.

Table 7.7 Number of accessions in each of the end groups in the diversity tree for *Cucumis sativus*.

Group	Accessions
Africa	195
East Asia	790
China	526
India	776
Nepal	27
Pakistan	92
South East Asia	373
West_Asia (except Turkey, Afghanistan and Iran)	276
Central_Asia	58
Afghanistan	41
Iran	140
Turkey	348
Europe	3376
North America	639
Russia	611

are different from those from Central and West Asia. The Central and West Asia populations cluster together with European and North American accessions. India is in a separate cluster, and accessions from India are very diverse. Most of these regions are fairly well represented at the global level in terms of the number of accessions, with the exception of Central Asia (see Table 7.7). Africa is less represented in terms of accessions, and the number of accessions from Afghanistan and Nepal is low, considering their proximity to India, which is a center for diversity for cucumber. It is difficult to say how well these accessions are spread geographically at a finer scale, as coordinate data for the collecting site are lacking for most of these accessions.

7.2.3 *Cucumis melo*

CWRs

According to Endl et al. (2018), the closest wild relatives of *Cucumis melo* are *C. picrocarpus* from Australia and *C. trigonus* from India. In the dataset combining Genesys, WIEWS and USDA-GRIN data, all 18 accessions of *C. trigonus* were collected in India and are conserved at IND001. In addition, 184 accessions of *C. callosus* collected from India are conserved *ex situ*; the Indian *C. callosus* is a synonym of *C. trigonus* (Endl et al. 2018). The same dataset includes no records for *C. picrocarpus*, from which we conclude that this important CWR is not conserved *ex situ*.

Landraces and cultivars

Passport information used to determine the horticultural group is available for only a small subset of *C. melo* accessions (see Table 7.8). However, based on

Table 7.8 Accessions of *Cucumis melo* divided by taxa. Landraces and cultivars are classified following Pitrat's (2016) horticultural groups.

Taxon	Biological status	Accessions
Cucumis melo L.	Cultivated	10,682
Cucumis melo subsp. melo L.	Cultivated	3,172
Cucumis melo L. group Makuwa	Cultivated	426
Cucumis melo L. group Conomon	Cultivated	391
Cucumis melo L. group Flexuosus	Cultivated	241
Cucumis melo L. group Momordica	Cultivated	202
Cucumis melo L. group Cantalupensis	Cultivated	170
Cucumis melo subsp. *agrestis* (Naudin) Pangalo	Cultivated	169
Cucumis melo var. *agrestis* Naudin	Wild	65
Cucumis melo var. *texanus* Naudin	Wild	45
Cucumis melo L. group Inodorus	Cultivated	27
Cucumis melo L. group Ibericus	Cultivated	22
Cucumis melo L. group Chito	Feral	3
Cucumis melo L. group Ameri	Cultivated	2
Cucumis melo L. group Dudaim	Cultivated	2
Cucumis melo L. group Cassaba	Cultivated	1
Cucumis melo L. group Kachri	Cultivated	1
Cucumis melo subsp. *orientale* Sageret ex Filov	Cultivated	1
Cucumis melo var. *cultus* Kurz	Cultivated	1

the information that is available, several horticultural groups are not well represented *ex situ*. Completing the passport data with this information would be an important step in assessing gaps in the conservation of horticultural groups.

In the choropleth map (Figure 7.7) that maps accessions according to their origin, Africa stands out as underrepresented in *ex situ* collections. Future explorations for *C. melo* germplasm should be directed toward increasing the representation of African germplasm, especially considering that there is a distinct African lineage of *C. melo* (Endl et al. 2018; Zhao et al. 2019).

Additional collections from India, including from a range of agroecological and agroclimatic subregions, are also desirable, because germplasm from India is diverse (Gonzalo et al. 2019) and has been an

important source of genes for resistance to disease and insects, as well as other agronomic traits. Germplasm explorations in other parts of Asia are also desirable.

7.2.4 Gourds: *Benincasa hispida, Cucurbita moschata, Lagenaria* spp., *Luffa* spp. and *Momordica* spp.

Filling the collection gaps for these gourds is a priority, for both national and international collections (WorldVeg). Additional collecting needs mainly concern landraces from centers of origin and diversity, many of which are threatened by the introduction of hybrid cultivars, as seen recently in many countries in South and Southeast Asia. Collection efforts could be undertaken jointly by national genebanks and the WorldVeg genebank. The main focus should be on collecting landraces in Bangladesh, Myanmar
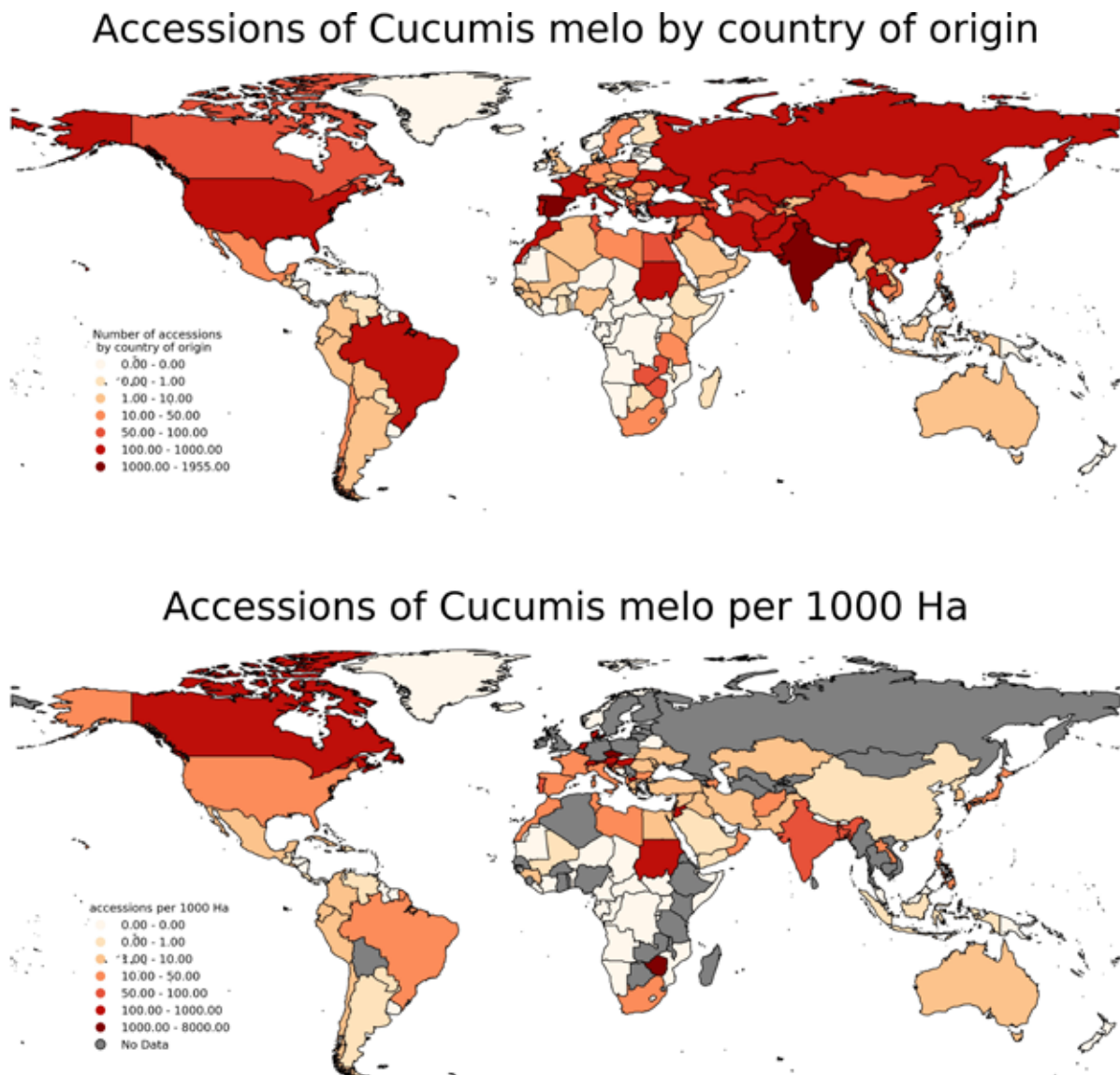
Figure 7.7 Above: Choropleth map of the raw number of accessions of *C. melo* according to their origin. Below: Choropleth map of the number of accessions per 1000 Ha of harvested area of *C. melo* according to their origin. Harvested area is the average between 1961 and 2019 (Source: FAOSTAT)

and Vietnam. Special attention should be given to aromatic *Luffa* and disease-resistance traits, in particular resistance to gummy stem blight in bottle gourd, begomoviruses and *Phytophthora* leaf blight. The market for sponge gourd prefers fruits characterized by high sweetness, good aroma and stickiness. Efforts are underway in Vietnam to develop pure aromatic inbred lines with elite fruit quality traits under plastic house conditions.

7.3 Collection vulnerability

Mexico

Cucurbita germplasm in Mexico is maintained by INIFAP (Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias) and SINAREFI (Sistema Nacional de Recursos Fitogenéticos) (see Table 7.9). SINAREFI is the official agency that funds collecting and collaboration among institutions in Mexico. Germplasm collections are distributed among several member institutions (INIFAP and different universities). SINAREFI is part of SNICS (Sistema Nacional de Inspección y Certificación de Semillas; National System of Seed Inspection and Certification) and is a member of UPOV and the International Seed Testing Association (ISTA). However, SINAREFI has no staff or budget allocated to *Cucurbita* (personal communication, Xitlali Aguirre-Dugua, Universidad Nacional Autónoma de México (UNAM), strategy expert consultation workshop, Thailand, 11–13 Dec. 2019).

There are serious problems with the quality of seed storage at INIFAP. Seeds are stored in a cold room at 4 °C and supposedly 10% relative humidity. However, humidity control is not working properly, leading to viability losses of up to 70%. Only 14% of *C. argyrosperma* accessions germinated, while germination rate of *C. moschata* was below 10% (personal communica-

tion, Xitlali Aguirre-Dugua (UNAM), strategy expert consultation workshop, Thailand, 11–13 Dec. 2019).

The rescue of the INIFAP and SINAREFI collections is of high priority. There are official plans to move the INIFAP collection to a new, modern genebank building at the Centro Nacional de Recursos Genéticos (CNRG) in Jalisco, which opened in 2012. A project for the regeneration and characterization of the INIFAP collection has been proposed since 2006 by Dr. Salvador Montes Hernández (responsible of the collection), intended to provide fresh and correctly characterized accessions to the CNRG. However, this proposal has not received support, mainly due to the absence of a long-term management and operation plan or an associated budget. Similarly, the SINAREFI *Cucurbita* collections, dispersed over several institutions, are endangered as they have not been regenerated and are losing viability (personal communication, Xitlali Aguirre-Dugua UNAM, strategy expert consultation workshop, Thailand, 11-13 Dec. 2019).

Table 7.9 *Cucurbita* germplasm maintained *ex situ* by INIFAP and SINAREFI.

Species	INIFAP	SINAREFI
C. argyrosperma	302	164
C. ficifolia	35	67
C. moschata	261	284
C. pepo subsp. *pepo*	189	132
Cucurbita spp.	31	78
Crop wild relatives	85	–
TOTAL	818	725

Source: Xitlali Aguirre-Dugua, Universidad Nacional Autónoma de México (UNAM), strategy expert consultation workshop, Thailand, Dec. 2019.
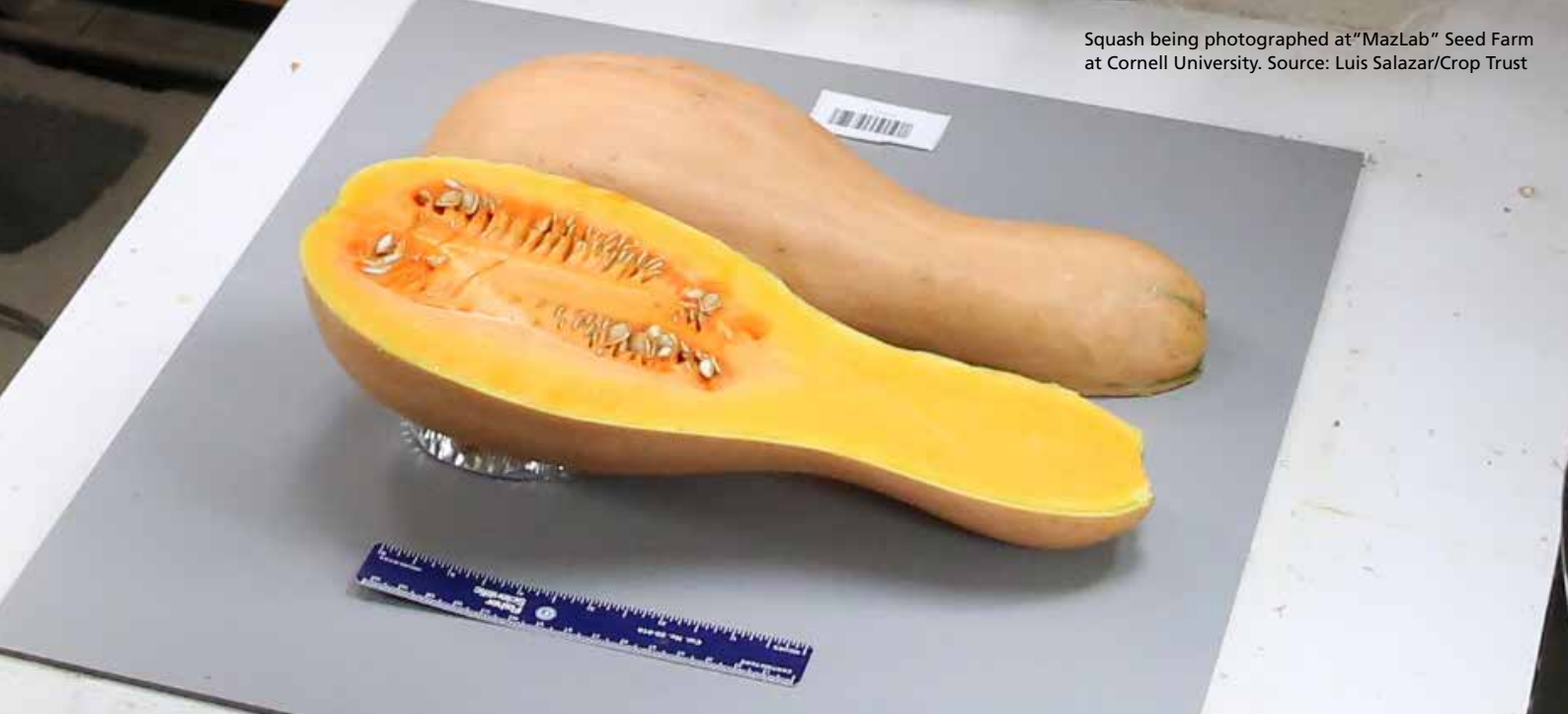
8 GERMPLASM CHARACTERIZATION AND EVALUATION

Ex situ collections are critical for the long-term conservation of the genetic diversity of crop species. However, without detailed information describing the diversity within collections, their usefulness for crop breeders, researchers and other users is severely limited. For this reason, the comprehensive characterization and evaluation of genebank accessions are essential. Characterization refers to the process of broadly describing accessions via distinct, identifiable traits, while evaluation refers to assessments of potential use for crop improvement. Generally, evaluation is more expensive and time consuming than characterization, as traits may be more complex and environmentally sensitive. Nonetheless, such precise phenotypic information allows for the efficient identification and use of accessions for breeding and other purposes. The inclusion of characterization and evaluation data in searchable databases further permits the easy identification of a group of accessions useful for an intended objective. Finally, the morphological and molecular characterization of accessions not only produces valuable agronomic data, but also helps to identify duplicates within and between collections (facilitating rationalization) and also major *ex situ* collection gaps.

A majority of the genebanks (80%) that responded to the Cucurbitaceae strategy survey had morphologically characterized their cucurbit collections; a minority (12%) had not yet characterized their collections, and the remaining 8% of respondents were unsure. In terms of evaluation, important cucurbit crop traits include resistance to biotic stresses (e.g., pests and diseases) and abiotic stresses (e.g., drought, heat and soil salinity). Screening for biotic stresses was reported to

be fairly common (conducted by 48% of genebanks), but screening for abiotic stresses was relatively rare (21% of genebanks). Therefore, large proportions of genebanks have yet to screen for any biotic or abiotic stresses (48% and 71%, respectively), which impedes the use of their collections for crop improvement.

In terms of challenges associated with characterization and evaluation, not all descriptors (i.e., sets of traits and their attributes) currently used by genebanks are relevant to farmers or breeders, as discussed in the strategy expert consultation workshop. To assist with this, images of the external fruit and internal sections should ideally be provided for each accession; however, most genebanks do not provide any such images (Narinder Dhillon, WorldVeg; strategy expert consultation workshop, Thailand, Dec. 2019). Furthermore, the publication of technical papers screening Cucurbitaceae crops is on the decline. There is a need for international screening efforts with standardized protocols (Antonio Monforte, CSIC, Spain; strategy expert consultation workshop, Thailand, Dec. 2019).

In the following sections, currently available descriptors are listed for the major Cucurbitaceae crops, with references to the literature for further information.

8.1 *Cucumis*

8.1.1 *Cucumis melo*

Muskmelon (*Cucumis melo*) cultivars are highly phenotypically diverse, particularly for fruit traits, as reviewed by Pitrat (2013). Major aspects of germplasm

characterization include: sex expression and flower morphology; fruit shape and size; fruit exocarp color and texture; fruit flesh color and flavor; seed coat characteristics; fruit maturation; and disease and pest resistance. Published lists of descriptors for muskmelon include those compiled by the following organizations:

- European Cooperative Programme for Plant Genetic Resources (ECPGR), Cucurbit Working Group
- International Plant Genetic Resources Institute (IPGRI)
- Union for the Protection of New Varieties of Plants (UPOV)
- USDA National Plant Germplasm System (NPGS)
- WorldVeg, Genetic Resources and Seed Unit (WorldVeg GRSU).

Recent decades have seen the publication of an abundance of molecular data and analyses for cucurbit crops, including muskmelon. These include sets of molecular markers useful for characterizing the genetic diversity and structure of collections, as well as physical and genetic maps essential for genetic analyses (Gonzalo and Monforte 2017). Such mapping studies have begun to elucidate the genetic basis of agronomically important traits, with multiple QTLs identified for traits such as yield; fruit color, morphology, and quality; and resistance to fungal and viral diseases (see Table 1 in Gonzalo and Monforte 2017 and references therein). A recent whole-genome resequencing project (Zhao et al. 2019) performed genome-wide association mapping to precisely identify loci related to fruit mass, bitterness and acidity, also showing the significance of different phenotypic and genotypic changes for independent domestication events.

8.1.2 *Cucumis sativus*

As discussed in the Cucurbitaceae strategy expert consultation workshop (Antonio Monforte, Thailand, Dec. 2019), major traits to be evaluated in cucumber (*Cucumis sativus*) include: fruit morphology (color, length, locule number and spine characteristics) and shelf life; leaf color and shape; parthenocarpy; plant architecture (e.g., determinate/indeterminate and branching); sex expression; and yield. Published lists of descriptors for cucumber include those compiled by the following organizations:

- ECPGR Cucurbit Working Group
- UPOV
- USDA NPGS
- WorldVeg GRSU.

As with muskmelon, a plethora of molecular resources are now available for cucumber, and more than 150 single gene traits have been described (Naegele and Wehner 2017), including for leaf morphology, parthe-

nocarpy, powdery mildew resistance and sex expression. Polygenic traits have also been described via QTL mapping, with multiple QTLs identified for traits such as earliness and flowering time; fruit bitterness, fragrance, shape and weight; and resistance to fungal and viral diseases (see Table 2 in Gonzalo and Monforte 2017 and references therein). More recently, genome-wide association studies (GWAS) have been implemented for cucumber, in order to finely dissect the genetic basis of horticulturally important traits. For example, Wang et al. (2018) applied a GWAS approach using more than 23K SNPs to identify genomic regions associated with the following traits: chilling tolerance, days to flower, disease resistance (anthracnose, downy mildew and gummy stem blight), fruit shelf life (weight loss, firmness loss and shriveling), fruit yield, root knot nematode resistance and root size.

8.2 *Citrullus*

Dessert watermelon (*Citrullus lanatus*) cultivars are extremely phenotypically diverse (Perkins-Veazie et al. 2012), varying in many fruit characteristics, such as color, shape, size, texture and flavor (see review in Paris 2015). Major aspects of germplasm characterization therefore include both fruit size and metrics of fruit quality, such as sugar content, flesh color and rind pattern (Li et al. 2018). As watermelon yields are highly susceptible to abiotic stress, and the low genetic diversity of cultivars makes them susceptible to pests and diseases, measures of yield (and its components), disease resistance and stress tolerance are also important agronomic traits (Hashizume et al. 2003). Within the genus, there are three additional minor crops (see Section 3.3), cultivated for different purposes: *C. amarus* (fodder), *C. colocynthis* (seed oil) and *C. mucosospermus* (nutritious seeds). As such, other traits (e.g., seed characteristics for *C. mucosospermus*) may be most important in the characterization of these crops, which may also serve as important reservoirs of disease resistance.

Published lists of descriptors for dessert watermelon (and in some cases other cultivated *Citrullus* spp.) include those compiled by the following organizations:

- ECPGR Cucurbit Working Group
- UPOV
- USDA NPGS.

Genetic mapping initiatives have been only recently implemented for watermelon, with the first QTL mapping study performed by Hashizume et al. (2003). However, such studies have since proliferated, with many QTLs identified for traits such as earliness and flowering time; fruit morphology (shape, weight, etc.) and color (both flesh and rind); fruit quality (espe-

cially sweetness); and disease resistance (see Table 3 in Gonzalo and Monforte 2017). Seed characteristics (e.g., oil content, size, shape, kernel percentage) have also been mapped for both *C. lanatus* and *C. mucosospermus* (Meru and McGregor 2013; Meru and McGregor 2014). More recently, whole genome resequencing data were used to perform GWAS for seven important fruit quality traits in watermelon (fruit shape, rind color, rind stripe, seed color, flesh color and bitterness) (Guo et al. 2019), identifying more than 40 genetic loci potentially modifying these traits. By resequencing accessions from other culti-vated *Citrullus* species, Guo et al. (2019) were also able to shed light on the domestication process, identifying signatures of selection for different loci during the process of domestication and improvement.

8.3 *Cucurbita*

The genus *Cucurbita* contains five cultivated species (*C. argyrosperma*, *C. ficifolia*, *C. maxima*, *C. moschata* and *C. pepo*). These crops are relatively distinct, being cultivated for different purposes and prized for different properties (OECD 2016). Depending on the species, the fruits produced may also be highly diverse, to the extent that they are classified into different horticultural groups (e.g., *C. maxima*; Decker-Walters and Walters 2000). Nonetheless, published descriptor lists are most often shared across the genus, though a few lists for individual cultivated species do exist. Pub-lished lists of descriptors for *Cucurbita* species include those compiled by the following organizations:
  • ECPGR Cucurbit Working Group
  • UPOV
    C. maxima
    C. moschata
    C. maxima × *C. moschata*
    C. pepo
  • USDA NPGS
    All *Cucurbita* species
    Squash (i.e., *C. maxima, C. moschata* and *C. pepo*)
  • WorldVeg GRSU.

To date, few genomic resources are available for *Cucurbita* species, which have been subject to less research interest in this regard than other major Cucurbitaceae crops (Gonzalo and Monforte 2017). High-quality linkage maps have only recently become available (Blanca et al. 2011; Esteras et al. 2012; Zhang et al. 2015) and were used to identify QTLs associated with flowering traits, fruit shape and fruit color (Esteras et al. 2012), along with vine length (an indicator of bush-type growth) (Zhang et al. 2015). New sequencing initiatives (for both the transcriptome and whole genome) for *C. maxima, C. moschata* and *C. pepo* will be crucial for advancing research and crop breeding efforts in these species.

8.4 Gourds

Gourds are a diverse group of cultivated species, mostly of local importance for smallholder farmers throughout South and Southeast Asia. Commercially important gourd species previously discussed in this strategy include: bitter gourd (*Momordica charantia*), bottle gourd (*Lagenaria siceraria*), snake gourd (*Trichosanthes cucumerina*), sponge gourd (*Luffa aegyptiaca*), ridge gourds (*Luffa acutangula*) and wax gourd (*Benincasa hispida*).

The UPOV has published descriptor lists for *Lagenaria siceraria* and *Momordica charantia.*

The USDA NPGS has published descriptor lists for *Lagenaria, Momordica* and *Trichosanthes* species. The descriptors include aspects of fruit morphology (e.g., length, presence of a neck, surface texture and unifor-mity of fruit color/shape/size/etc.) and phenology.

In addition, WorldVeg has published much more com-prehensive descriptor lists for the following five gourd genera:
  • *Benincasa*
  • *Lagenaria*
  • *Luffa*
  • *Momordica*
  • *Trichosanthes.*

During the development of this Cucurbitaceae strategy, the following additional important descrip-tors for gourd germplasm were highlighted (Antonio Monforte, strategy expert consultation workshop, Thailand, Dec. 2019):
  • Nutritional content
  • Potential use as rootstock
  • Use in traditional medicine
  • Waxy bloom.

8.5 *Sechium*

The genus *Sechium* contains one minor crop species, the chayote (*Sechium edule*), a popular tropical fruit originally native to Mexico. Within the crop species, there are a number of morphological types, each quite unique in appearance; however, only the smooth, green "*virens levis*" type is commercially cultivated (Vieira et al. 2019). The first set of descriptors for chayote fruits was published by Engels (1983) and included aspects of fruit shape, size and weight. More recently, the USDA NPGS published a descriptor list for gourds (also very focused on fruit morphology) that is also applicable for chayote. A more comprehensive descriptor list covering leaf, flower and fruit traits was created by Cadena-Iñiguez et al. (2008) to describe infraspecific variation in *S. edule* within Mexico.

9 GERMPLASM DISTRIBUTION

All genebanks that participated in the Cucurbitaceae strategy survey reported distributing germplasm and keeping records of distributions made. Twenty-one genebanks provided estimates of the average number of accessions distributed on an annual basis, both within and outside the country where the genebank is located. Among these genebanks, distribution within the country was more common (n = 21/21 respondents) than outside the country (n = 14/21). Within the country, genebanks distributed an average of 465 accessions annually (range = 3 to 2,664 accessions). Outside the country, genebanks distributed an average of 469 accessions annually (range = 0 to 4,798). The WorldVeg genebank (Taiwan) and USDA genebanks (Griffin, GA and Ames, IA) were the largest distributors. Eighty percent of genebanks require a Material Transfer Agreement (MTA) for the distribution of germplasm, while 16% distribute germplasm without requiring an MTA; the remaining 4% reported being unsure of their terms and conditions for distribution.

Germplasm was distributed to a variety of user groups (Figure 9.1). The main recipients of germplasm are academic researchers, plant breeders and farmers and farmer organizations. Genebanks reported using the following means to inform potential germplasm users of the availability of accessions and related data:

- Online information systems/platforms specific to the genebank with passport data and, in some cases, characterization and evaluation data
- Various national, regional and international databases not specific to the genebank

Accessions distributed annually by user (n = 16)
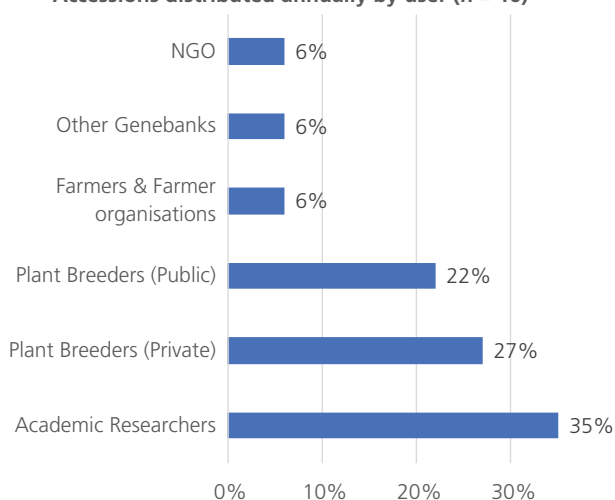
Recipients of distributed material (average among genebanks)
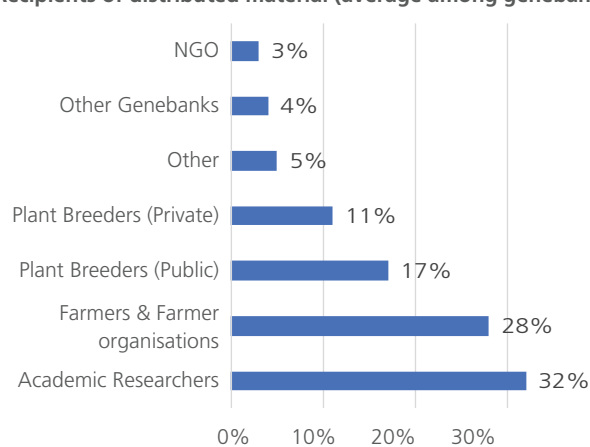
Figure 9.1 above: Percentage of accessions distributed annually by type of germplasm user, based on data from 22 genebanks that responded to the survey. Note that bars represent average values of percentages reported by individual genebanks and as such do not sum to 100%. below: Percentage of accessions distributed annually by type of germplasm user, based on data from 16 genebanks that provided information both on the number of accessions distributed annually and on what types of users received germplasm distributions

- The GRIN-Global National Plant Germplasm System website (managed by the USDA)
- Training programs, workshops and other teaching activities
- Seed catalogs, and seed and diversity fairs
- Scientific articles and technical publications
- Information sent upon request via email.

The majority (72%) of genebanks indicated that the Cucurbitaceae germplasm held in their collections is available in sufficient quantity and health for distribution, but this was not the case for 24% of genebanks; the remaining 4% were unsure. Sixteen percent of genebanks reported problems with disease in their collections, which may restrict germplasm distribution.

Additional factors limiting distribution listed by the genebanks include the following:
- Low quantity of seed preserved per accession OR seed unavailable for distribution due to a backlog in regeneration (reason given by n = 6 genebanks)
- Incomplete passport information AND/OR incomplete characterization (morphological and/or molecular) and evaluation data (n = 5)
- Unmet import requirements/phytosanitary regulations in country of requestor (n = 2)
- Low seed viability (n = 1)
- Lack of online information/access for genebank materials (n = 1)
- Poor sanitary condition of germplasm (e.g., presence of seedborne pathogens that are difficult to eradicate) (n = 1)
- Limited regional interactions with farmers, farmer groups and companies (n = 1)
- Lack of funding (n = 1).

9.1 Procedures for distribution

The majority of genebanks surveyed have adequate procedures in place for phytosanitary certification (64%), packaging (71%) and shipment (64%) of germplasm materials for distribution (Figure 9.2). Sixty percent of genebanks do not charge the requestor for germplasm distribution; however, 8% of genebanks charge for the cost of the seed samples, 24% for the cost of shipment and 8% charge for both (seed samples and shipment). The USDA NPGS represents a particularly important public germplasm resource, with open access to breeders and researchers worldwide. Distributing about 250,000 samples per year, the NPGS distributes germplasm both nationally and internationally at no cost to the requestor. Orders are placed online through GRIN-Global and a Standard Material Transfer Agreement (SMTA) must be signed for international request (Colin Khoury, strategy expert consultation workshop, Thailand, 11–13 Dec Dec. 2019).

9.2 Evolving distribution patterns

To assess how patterns of distribution may change over the next three to five years, genebank curators were asked to make predictions for the number of cucurbit accessions distributed both nationally (i.e., within the country where the genebank is located) and internationally (i.e., to other countries). Of the genebanks that made predictions, a majority foresaw increases in distribution: 58% expected an increase in the number of accessions distributed nationally and 35% an increase in distributions to other countries (Figure 9.3). However, 52% of genebanks were not able to predict how distribution to other countries may change in the near future.
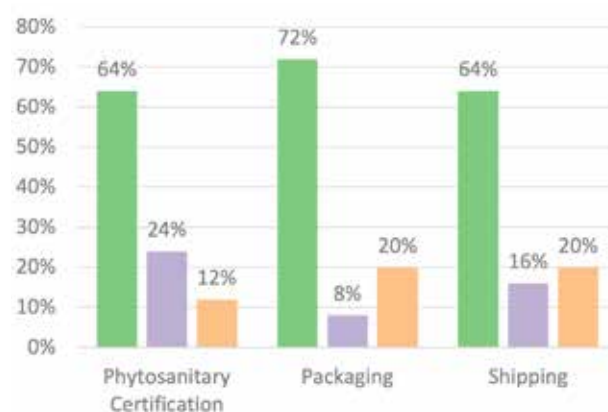
Figure 9.2 Availability of adequate procedures for phytosanitary certification, packaging and shipment of germplasm materials for distribution, as reported by genebanks in the survey.
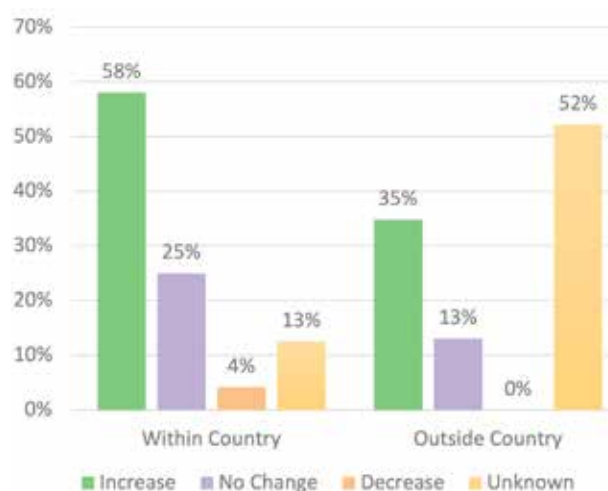
Figure 9.3 Projected changes to germplasm distribution within the next three to five years, both for distributions made within the country where the genebank is located and to other countries, as reported by genebanks in the survey.

Lang Kürbs - *Lagenaria siceraria*. 1543. Source: Leonhart Fuchs/Wikimedia

Lang Kürbs.

CCIX.

Cucurbita oblonga.
Cucumis flexuosus.

10 DOCUMENTATION AND GERMPLASM MANAGEMENT

International and regional genebanks typically develop quality management systems (QMS) to document procedures carried out by genebank staff and ensure that standard protocols are followed. This practice is encouraged for national genebanks as well. A QMS aligns genebank procedures with international standards published by FAO, describing all necessary activities to meet policy and technical standards. It also outlines ways to effect continual improvement in the genebank's administrative, operational and technical performance. This provides critical information for genebank users, regulatory bodies and donors, allowing them to evaluate genebank competence, effectiveness and efficiency.

Documentation and data availability are a key genebank performance indicator. Collection data must be made available online for easy access by potential users, thus enabling informed choices of accessions most suitable for user purposes. During the Thailand expert consultation meeting (Dec. 2019), it was stressed that there is a need to improve passport data for Cucurbitaceae collections; the registration of donor data for accessions introduced from other genebanks is especially important to avoid duplication. Regeneration protocols for Cucurbitaceae crops should also be shared and harmonized. Lastly, there is a need for widespread adoption of better germplasm management systems that follow international genebank standards (e.g., on germination practices).

10.1 Results of the Cucurbitaceae strategy survey

The majority of surveyed genebanks reported having written procedures in place to describe key genebank and germplasm management processes (Table 10.1). The best documented practice is regeneration, with 88% of genebanks having written regeneration protocols, while the least documented processes are associated with germplasm health assessment (40%). Thirty-nine percent of genebanks are willing to share their written procedures with the Crop Trust, 48% are unsure about providing a copy and 13% declined to share these documents.

A majority of responding genebanks (84%) reported using an electronic information system for managing their collection, for example, to store and access data related to distribution, germination, germplasm storage and other topics. A further 12% of genebanks are using such an information system only in part (i.e., for a subset of genebank-related processes and activities), while 4% of genebanks have no electronic system. A significant number of genebanks have already switched to using GRIN-Global (n = 6) as an information management system, with others planning to make the switch shortly; one other genebank has adopted a modified version of GRIN-Global. Other information management systems currently in use are: AVGRIS (used by WorldVeg), BIOGEN, DB Germo Web,

Table 10.1 Proportion of genebanks with written procedures and protocols for critical genebank and germplasm management processes.

Genebank or germplasm management process	Genebanks with written guidelines	Number of respondents
Regeneration	88%	23
Characterization	85%	22
Storage and maintenance	85%	22
Documentation	85%	22
Distribution	81%	21
Acquisition (including collecting, introduction and exchange)	77%	20
Safety duplication	77%	20
Germplasm health	42%	11

Note: Responses to this question were received from 26 out of 28 survey respondents.

GENIS (used by CGN), the PGR Portal (.Net Programme) and SDIS/SDB. Other genebanks use dedicated software or Microsoft Office software, such as MS Excel, MS Access and MS FoxPro.

Fifty-two percent of genebanks reported that they make information on their Cucurbitaceae collections fully accessible online, while 24% of genebanks make such information partly accessible online; the other 24% of genebanks do not yet offer online access to collection information. The majority of genebanks have passport data available electronically (76% to a large extent), followed by characterization data (28%) and evaluation data (20.8%) (Figure 10.1).

Collection data for a significant number of genebanks are also included in other national, regional and/or international databases (Figure 10.2). Importantly, a full 50% of genebanks upload accession-level information (usually passport information at a minimum) to international databases, such as Genesys and/or WIEWS, a trend to be encouraged.

10.2 A special case: the European Cucurbits Database

A European Cucurbit Working Group (WG) was formed in January 2002, at a meeting of partners in Adana, Turkey, to strengthen collaboration on Cucurbitaceae genetic resources. For further information on the Cucurbit WG. One of the key goals of the Cucurbit WG was the creation of a dedicated European Cucurbits Database (ECCUDB; currently available online).

As of November 2010, the ECCUDB contained searchable passport data for 27,489 accessions representing 21 genera and 72 species. *Cucumis* accounted for 42% of these accessions, *Cucurbita* for 30% and *Citrullus* for 25% (Diez 2011). Characterization data, including images, were also available for a small subset of accessions: *Cucumis sativus* (n = 775), *Citrullus lanatus* (107) and *Cucurbita pepo* (53). The data were contributed by 39 institutions from 23 countries. Other information provided included descriptions of the donor institutes and descriptors used, as well as resources on cucurbit taxonomy and *in situ* conservation. At the time, it was planned to improve the quality of pass-

port and characterization data, both by uploading new data and by reviewing the existing information.

The ECCUDB data are currently available for offline download and use, but the database is no longer being updated. The Cucurbit WG aims to eventually integrate the data into EURISCO, but this has yet to be done.
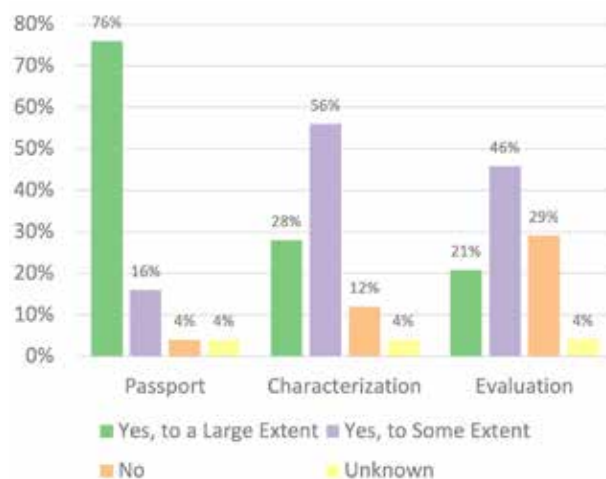
Figure 10.1 Availability of accession-level passport, characterization and evaluation data in electronic format, as reported by genebanks in the Cucurbitaceae strategy survey.
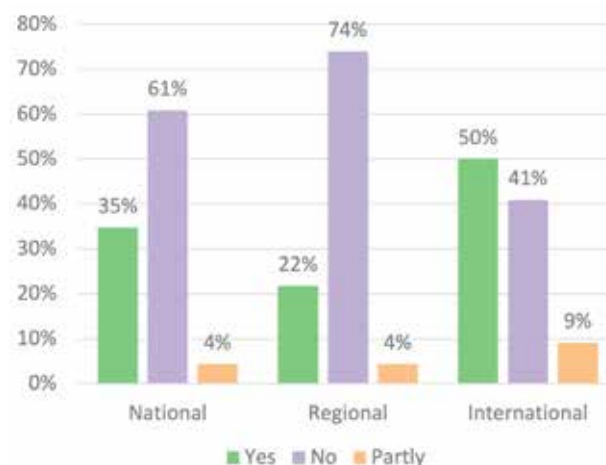
Figure 10.2 Percentage of genebanks that upload accession-level information to external national, regional and international databases, as reported by genebanks in the Cucurbitaceae strategy survey.

11 BREEDING GOALS FOR CUCURBITACEAE CROPS

As a result of domestication and crop improvement bottlenecks, modern crop species have experienced reductions in genetic diversity. These diversity losses can be substantial, with some crops faring worse than others (Doebley et al. 2006; Meyer and Purugganan 2013). Many Cucurbitaceae crops show relatively high reductions in diversity, compared to other crop species; part of this variability is likely due to differences in the severity of population bottlenecks experienced by crops of different types, with fruit crops seeing smaller population sizes (and hence greater diversity losses) than grain crops, for example (Qi et al. 2013). As a result, the narrow genetic base of many modern crop cultivars represents a challenge for food security and sustainable crop development. Without ample genetic diversity from which to select, breeders may struggle to find variation for abiotic and biotic stress resistance, putting crop yields at risk.

However, additional genetic variation (and related phenotypes of agronomic interest) may be preserved in landraces and CWRs. The potential of CWRs as a source of genetic variation for crop improvement has long been recognized, but only routinely utilized in recent decades (Dempewolf et al. 2017). By crossing crop species with their CWRs, breeders can reintroduce novel and potentially beneficial variation. However, the process of successfully transferring traits of interest into the crop is not without its challenges,

which range from poor interspecific crossability to the unintended transfer of deleterious diversity in the form of undesirable traits linked to the trait of interest (Zamir 2001). Successful crop improvement using wild diversity thus relies on a number of factors, including crossing barriers and species relationships, modes of reproduction, the genetic basis of the trait of interest, screening procedures and their efficiency, and the availability of genetic resources and/ or transformation systems for the crop (Stalker 1980; Mammadov et al. 2018). For example, the simpler the genetic basis (ideally only one or two genes), the easier it is to introduce a trait of interest into cultivated lines. As a result, CWRs have largely been exploited for only monogenic traits to date, as more complex traits (e.g., aspects of quality, stress tolerance and yield) may not be technically feasible (Zamir 2001).

Under climate change and its anticipated stresses on cultivated systems, the availability of genetic variation for agronomically important traits will be of paramount importance to sustain crop yields. Thus, reliance on CWRs in breeding programs is expected to increase in future. To facilitate the utilization of diversity from across crop gene pools (including CWRs, landraces, traditional varieties, etc.), the secure conservation, characterization (and potentially evaluation) and easy accessibility of germplasm will be

instrumental. Improved technologies, such as genomics-assisted breeding, will also be critical to overcome technical challenges with accessing and using this diversity. To enhance yield durability, many favorable traits may need to be combined in a single cultivar, such as cultivars that are resistant to multiple diseases.

In this section, a brief overview of past and present breeding goals is presented for the major Cucurbitaceae crops, with a focus on current challenges. Major pests and diseases are discussed for each crop, and examples of successful crop improvement highlighted. Complementary to the information in Section 5, important sources of resistance genes (such as CWRs) are described.

11.1 *Citrullus lanatus*

Watermelon domestication and improvement have produced early-maturing, more compact plants, yielding large fruits full of sweet, edible flesh (see Section 4 and Wehner 2008). While high yields and fruit quality are universally prized, there is substantial regional variation in desirable fruit characteristics (and hence breeding goals), as a result of diverse consumer preferences. For example, breeding programs in China and the USA have produced distinctly

different cultivars: Chinese cultivars have small-to-medium-sized, globular fruits with a thin rind, while American cultivars have large, oblong fruits with a thick rind (Sheng et al. 2012; Guo et al. 2013). As such, cultivars from different geographic regions have genetically differentiated over time. For example, in a recent molecular analysis based on simple sequence repeat (SSR) markers (Sheng et al. 2012), Russian and US cultivars were found to be closely related, and to form a separate genetic group from Chinese and Japanese cultivars. Even within regions, desirable fruit characteristics may vary among cultivars bred for different purposes (e.g., local sales versus long-distance shipment) or among specialty types (e.g., bred for a variety of fruit flesh colors, sizes, etc.) (see Wehner 2008 for an overview). For example, in the USA, seedless varieties (triploid hybrids) are becoming popular, and these are smaller, with higher-quality flesh than seeded varieties.

A broad range of fungal, bacterial and viral diseases affect watermelon productivity worldwide (Table 11.1), causing substantial yield losses and reductions in fruit quality (Sharma et al. 2016; Levi et al. 2017). Breeding cultivars with resistance to these diseases is an important long-term objective for watermelon improvement programs (Jarret et al. 1996), although

Table 11.1 Important globally distributed diseases that affect watermelon crops.

	Pathogen	Specificity	References
Fungal diseases			
Anthracnose	*Colletotrichum orbiculare* (Berk. & Mont.) Arx.	All cucurbits	Wasilwa et al. 1993; Boyhan et al. 1994; Maynard and Hopkins 1999; Gan et al. 2013
Downy mildew	*Pseudoperonospora cubensis* (Berk. & Curt.) Rostovtsev	Most cucurbits	Lebeda and Cohen 2011; Cohen et al. 2015
Fusarium wilt	*Fusarium oxysporum* f. sp. *niveum* (E.F. Sm.) Snyder & Hansen	Specific to watermelon	Zhou et al. 2010; Egel and Martyn 2013; Petkar et al. 2019; Roberts et al. 2019; Hudson et al. 2020
Gummy stem blight	*Didymella bryoniae* (Auersw.) Rehm	All cucurbits	Gusmini et al. 2005 2017; Stewart et al. 2015; Li and Brewer 2016
Powdery mildew	*Erysiphe cichoracearum* (D. ex. Merfat) and *Podosphaera xanthii* (Castagne) Braun & Shishkoff	All cucurbits	Davis et al. 2001; Thomas et al. 2005; Tetteh et al. 2013
Bacterial diseases			
Watermelon fruit blotch	*Acidovorax citrulli* (Schaad et al.) Schaad et al.	All cucurbits, but most severe in watermelon	Bahar and Burdman 2010; Burdman and Walcott 2012; Zivanovic and Walcott 2017; Daley and Wehner 2020
Viral diseases			
Papaya ringspot virus	Papaya ringspot virus – watermelon strain	All cucurbits	Strange et al. 2002; Guner 2004; Gonsalves et al. 2010; Levi et al. 2016
Watermelon mosaic virus	Watermelon mosaic virus	All cucurbits	Gillaspie Jr. and Wright 1993; Ali et al. 2012; Rajbanshi and Ali 2016
Zucchini yellow mosaic virus	Zucchini yellow mosaic virus	Most cucurbits	Provvidenti 1991; Guner 2004; Guner et al. 2018

improved cultural and chemical approaches to disease management on farm are also important (Sharma et al. 2016).

In the case of major fungal diseases, resistance to anthracnose and Fusarium wilt has been incorporated into several commercial cultivars, although only for a subset of races (Wehner 2008; Martyn 2014). For example, four races are currently recognized for Fusarium wilt, but high-level resistance is only available for two of the races (race 0 and 1) (Egel and Martyn 2013); resistance to races 2 and 3 is therefore a priority for watermelon breeders (Petkar et al. 2019). For other fungal diseases (e.g., downy mildew, gummy stem blight and powdery mildew), there are no resistant commercial cultivars or hybrids available, and control measures rely on the use of fungicides (Jarret et al. 1996; Tetteh et al. 2010; Savory et al. 2011; Gusmini et al. 2017; Damicone and Brandenberger 2020). In the case of both downy mildew and powdery mildew, this is at least partly due to the recent emergence of new, highly virulent genotypes, races and pathotypes (Davis et al. 2001; Cohen et al. 2015; Thomas et al. 2017). In Asia, where the bulk of watermelon production occurs (Section 2), a type of sudden wilt also affects watermelon yields (John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019). While poorly understood, sudden wilt is likely mediated by interactions between poor environmental conditions (e.g., drought or waterlogging) and plant fungal pathogens (e.g., *Fusarium, Pythium* and *Rhizoctonia*).

Watermelon crops are also susceptible to bacterial diseases, such as watermelon fruit blotch, and viral diseases, such as those caused by the potyviruses (see Table 11.1). Watermelon fruit blotch is a highly destructive pathogen that currently threatens global watermelon production (Bahar and Burdman 2010; Burdman and Walcott 2012); there are currently no commercial cultivars with resistance, although screening efforts are underway (Daley and Wehner 2020). Viral pathogens, such as PRSV, WMV and ZYMV, affect watermelon yields worldwide by reducing fruit set (Guner and Wehner 2008; Damicone and Brandenberger 2020). Control of viral diseases also remains challenging, as current commercial cultivars are not resistant and the diseases themselves remain understudied in watermelon (Levi et al. 2016; Guner et al. 2018; Damicone and Brandenberger 2020). Future breeding goals should include multiple virus resistance, as mixed infections are common (Xu et al. 2004). In Asia, melon yellow spot virus (MYSV), watermelon bud necrosis virus (WBNV) and watermelon silver mottle virus (WSMoV) are also problematic (Chia Tai Seed Co. data; John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019).

In many cases, genetic diversity for resistance to the above pathogens has been described in existing collections of crop cultivars and CWRs (e.g., Gillaspie Jr. and Wright 1993; Strange et al. 2002; Thomas et al. 2005; Davis et al. 2007; Guner and Wehner 2008; Tetteh et al. 2010; Daley and Wehner 2020). For example, the minor crop species citron melon (*C. amarus*) and egusi melon (*C. mucosospermus*) provide valuable sources of resistance to powdery mildew, and citron melon holds resistance to anthracnose, Fusarium wilt and gummy stem blight (see review in Levi et al. 2017), as well as watermelon fruit blotch (Daley and Wehner 2020) and a number of potyviruses (such as those in Table 11.1. The colocynth (*C. colocynthis*) may also represent an important source of resistance to PRSV (Levi et al. 2016). These three species are cross-compatible with dessert watermelon (*C. lanatus*) (see Section 5), and thus have great potential for use in breeding efforts. Various cultivated and wild *Citrullus* taxa may also hold valuable alleles for abiotic stress resistance, such as to cold, drought and heat stress (Levi et al. 2017).

As discussed in Section 2, watermelon cultivars exhibit a particularly narrow genetic base compared to many other crops, even those in the Cucurbitaceae (Levi et al. 2001). As such, it may be particularly important to use genetic diversity from landraces, traditional varieties and CWRs, as breeding efforts seek to introduce new diversity into the watermelon gene pool (Guo et al. 2013). Breeding approaches that rely on hybrid vigor (or heterosis), popular for other crops, are also of less importance for watermelon, as inbreds typically perform as well as hybrids (Wehner 2008). One exception is in the production of seedless watermelons (triploid hybrids), or when needing to combine two dominant traits (e.g., resistance to multiple diseases).

11.2 *Cucumis sativus*

As is the case for watermelon, breeding goals for cucumber tend to vary among regions and markets (Tatlioglu 1993), though increasing yields and fruit quality are universally important. Two basic cucumber types, those consumed fresh ("slicing" cucumbers) and those consumed as processed products ("processing" or "picking" cucumbers), have different requirements, especially as the crops are cultivated and harvested differently. Within these two categories, major fruit types are reviewed by Staub et al. (2008) for different regions (e.g., Europe versus the USA). In addition to the major fruit types, region-specific specialty types also exist, such as "mini" and "snack" types, or even "lemon" cucumbers (bright yellow and shaped like a lemon). However, despite the phenotypic diversity seen in cucumber cultivars, cucumber is quite depauperate genetically, as revealed by recent molecular studies (Lv et al. 2012; Qi et al. 2013). In particular,

many cucumber cultivars share disease resistance obtained from the same source (same genetic basis), a substantial threat to the industry in case of the emergence of novel disease strains and/or races (Clark et al. 1996). However, resistance to certain diseases, such as CMV, powdery mildew and scab, has endured for decades.

Disease resistance, and the maintenance of resistance, has long been an important goal of cucumber improvement (Naegele and Wehner 2017). For example, in the USA, cultivars resistant to a variety of diseases (e.g., angular leafspot, anthracnose, CMV, powdery mildew and scab; see Table 1 in Staub et al. 2008) have been developed since the early 1900s. In many cases, resistance had a relatively simple genetic basis (one to a few genes), facilitating its incorporation into elite cultivars. Nonetheless, it remains important to identify new sources of resistance, owing to the problems with genetic uniformity discussed above. According to Chia Tai Seed Co. (John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019), cucumber germplasm with resistance to the following fungal diseases is needed: anthracnose, downy mildew, Fusarium wilt (*Fusarium oxysporum* f. sp. *cucumerinum* J.H. Owen), powdery mildew, scab (*Cladosporium cucumerinum* Ell. & Arth.) and target leaf spot (*Corynespora cassiicola* (Burk. & M.A. Curtis) C.T. Wei.). Downy mildew is currently particularly problematic in cucumber, causing heavy yield losses; as discussed for watermelon, this disease has re-emerged since the early 2000s (Cohen et al. 2015), and previously resistant cultivars have now become susceptible. As high levels of downy mildew resistance have not been found in cultivated cucumber (Olczak-Woltman et al. 2011), one option may be to utilize resistance from other *Cucumis* species, for example *C. hystrix* (Chen et al. 2004).

Another disease of concern for cucumber production is bacterial wilt (*Erwinia tracheiphila* (E.F.Sm.) Holland; Shapiro et al. 2018), particularly in South and Southeast Asia, the main production regions for cucumber. A number of viral diseases also merit further research into sources of resistance (John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019): cucumber green mottle mosaic virus (CGMMV), cucumber vein yellowing virus (CVYV), cucurbit yellow stunting disorder virus (CYSDV), MYSV, PRSV, ToLCNDV and ZYMV. Work on insect pests in cucumber is ongoing, as there is little genetic resistance in modern cultivars (Staub et al. 2008), with one exception: resistance to root-knot nematodes (*Meloidogyne javanica* (Treub) Chitwood) was introgressed into modern breeding lines from the wild progenitor, *C. sativus* var. *hardwickii*. Nematode-resistant rootstocks (e.g., *Cucumis metuliferus*, *Cucurbita* spp. or *Lagenaria* spp.; see El-Eslamboly and Deabes 2014) may also be used

to ameliorate cucumber yield losses caused by nematodes. Cucumber grafting is an important cultivation technique, not only for pest resistance, but also to overcome soilborne diseases and reduce abiotic stress. For example, an accession of *Cucurbita ficifolia* that is both tolerant of low temperatures and resistant to Fusarium wilt is being used as a highly successful rootstock for cucumber cultivation in China (Haiping Wang, CAAS, Beijing, China; strategy expert consultation workshop, Thailand, Dec. 2019).

Interestingly, the nutritional value of cucumber might be enhanced by introgressing genes from the beta-carotene-rich Xishuangbanna gourd (*C. sativus* var. *xishuangbannanensis*) into common cucumber cultivars. This has been successfully done for the US pickling cucumber industry (Cuevas et al. 2010) and for cucumber production in China (Haiping Wang; strategy expert consultation workshop, Thailand, Dec. 2019). In US pickling cucumbers, progeny segregation analyses have revealed a relatively simple genetic basis to beta-carotene content in cucumber fruit flesh: two recessive genes in the mesocarp, and one recessive gene in the endocarp (Cuevas et al. 2010). In China, a QTL analysis undertaken by CAAS identified three QTLs related to beta-carotene content, contributing 52.8%, 22.0% and 8.2%, respectively, to the total phenotypic variance (Haiping Wang; strategy expert consultation workshop, Thailand, Dec. 2019).

11.3 *Cucumis melo*

Muskmelon is a highly diverse crop, comprising many cultivar groups (see Section 3.1) with fruits that vary dramatically in size, shape, color, flavor and texture. As with cucumber, local preferences for specific melon types shape regional goals for breeding programs. However, increased yield (and yield durability), improved fruit quality and taste, and long shelf life are major goals irrespective of type. Climacteric ripening (i.e., fruits continue to ripen and soften after harvest) is found in many cultivar groups, such as the popular 'Cantalupensis' group, and is associated with a short shelf life (Moreno et al. 2008). Therefore, a major objective of breeding programs is to increase the shelf life of climacteric melons, without sacrificing fruit aroma or flavor (Fernández-Trujillo et al. 2011; Farcuh et al. 2020).

An important aspect of yield durability in muskmelon is disease resistance, long a critical element of cultivar development (Pitrat 2008). Many of the same diseases affecting cucumber are also problematic for muskmelon; for example, fungal diseases such as downy mildew, Fusarium wilt, gummy stem blight, powdery mildew and scab commonly affect muskmelon crops. While many resistant cultivars are available for some fungal diseases, such as powdery mildew (though new

problematic races may emerge over time; McCreight et al. 2012), there are few resistant cultivars for others, such as downy mildew. Currently, Fusarium wilt (*Fusarium oxysporum* f. sp. *melonis* (Leach & Currence) Snyd. & Hans) is one of the most devastating of the soilborne diseases, for which there are no chemical controls and a limited number of commercial cultivars with resistance (and this may be to only one or a subset of races) (Sebastiani et al. 2017); however, grafting onto resistant rootstocks (such as various *Cucurbita* species and hybrids) can provide adequate protection (Ramos et al. 2015). Grafting is a commonly used technique in muskmelon to enhance resistance to soilborne fungal diseases, to which muskmelon is particularly susceptible (Ambrósio et al. 2015). In South and Southeast Asia, where the majority of melon production occurs, a type of fungally mediated sudden wilt is also problematic (see discussion for watermelon), as are bacterial fruit blotch (*Acidovorax citrulli*) and bacterial wilt (*Erwinia tracheiphila*) (John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019).

The control of viral diseases in muskmelon is also challenging, as few commercial resistant cultivars are available and mixed infections are common. In some cases, for example that of cucumber mosaic virus (which also affects muskmelon), resistance might be strain-specific or environmentally dependent (e.g., relying on temperature; Zitter and Murphy 2009; Pascual et al. 2019). Other problematic viral diseases in muskmelon include: CYSDV, melon necrotic spot virus (MNSV), MYSV, ToLCNDV and the potyviruses (PRSV-W, WMV and ZYMV; see discussion for watermelon). Cucurbit yellow stunting disorder virus is a recently emerged crinivirus of high priority for muskmelon production (Wintermantel et al. 2016); several sources of resistance have been identified to date, but all appear to be under the control of recessive genes (McCreight et al. 2017).

11.4 *Cucurbita*

As discussed in previous sections, *Cucurbita* includes several economically important crop species, including crops commonly referred to as pumpkins, squash and gourds. Selection for fruit shape and color has been an important part of the development of modern cultivars and remains relevant to current breeding programs. The wide diversity of fruit types for each *Cucurbita* crop is reviewed in Section 2.4 (or see Ferriol and Picó 2008 for further detail). Heightened fruit quality, productivity and earliness are also important goals of crop improvement. Higher productivity and earliness may be achieved through changes to plant architecture. For example, following the discovery of a genetic variant in *C. pepo* responsible for a non-

vining, or "bushy," growth habit (*Cucurbita* species are normally vines), bush-type *C. pepo* cultivars were developed for several fruit types, and the trait has also been introduced to *C. moschata* (Ferriol and Picó 2008; Paris 2008). More compact plants have earlier flowering and higher yields, though fruits may sometimes be smaller. For yield stability, resistance to abiotic stresses (such as cold) and biotic stresses (in the form of pests and diseases) is also critical (Robinson 1995).

Disease resistance, especially to viral diseases, may well be the most important goal for *Cucurbita* crop improvement. Acquiring lasting resistance to viral diseases is particularly challenging, as the most problematic viruses tend to vary regionally and also over time, with new diseases and/or strains of existing diseases constantly emerging (Paris 2017). Moreover, viruses cause many of the most destructive diseases in *Cucurbita*, and certain crops, such as summer squash (*C. pepo*), are especially vulnerable, as they are harvested continually over a long growing season. In terms of specific diseases, while there is some variability among crop species, aphid-transmitted potyviruses (e.g., CMV, PRSV, WMV and ZYMV) are generally problematic in *Cucurbita* (Ferriol and Picó 2008), with ZYMV being the most destructive in recent decades (Capuozzo et al. 2017). Another viral disease, squash leaf curl virus, is also becoming increasingly important (Brown et al. 2002), particularly in warmer regions. As with other cucurbit crops, the majority of pumpkin, squash and gourd production occurs in South and Southeast Asia, where MYSV, squash leaf curl China virus, ToLCNDV and tomato yellow leaf curl Thailand virus (TYLCThV) also affect production (John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019). *Cucurbita* crops are also affected by bacterial diseases (e.g., angular leaf spot, bacterial leaf spot and *Phytophthora* fruit rot) and, to a lesser degree, fungal diseases (e.g., downy mildew, gummy stem blight and powdery mildew). Leaf silvering, induced under drought stress by whiteflies (*Bemisia tabaci* (Gennadius)), may also drastically reduce crop performance (Paris 2017).

For both cultivated and wild *Cucurbita* species, susceptibility to the diseases discussed above can vary substantially, not only among, but also within, species. For example, *C. pepo* has little natural resistance to ZYMV and the other potyviruses, but resistant commercial cultivars have been developed by introgressing resistance genes from *C. moschata*. In fact, *C. moschata* is an important reservoir of resistance to many pathogens, including CMV, Fusarium wilt, PRSV, ToLCNDV and WMV, as well as ZYMV (Traka-Mavrona et al. 2000; Brown et al. 2003; Sáez et al. 2020). Resistance genes may also be obtained from crop wild relatives, such as *C. ecuadorensis* and *C. okeechobeensis*.

In the case of *C. ecuadorensis*, potyvirus resistance was transferred to the crop *C. maxima* (Herrington et al. 2001), while powdery mildew resistance from *C. okeechobeensis* has been used to develop resistant *C. moschata* and *C. pepo* commercial cultivars (Cho et al. 2003; Formisano et al. 2010). As such, interspecific crosses represent an essential element of *Cucurbita* breeding programs, although they are not made without difficulty, given interspecific barriers to hybridization (see Section 5.2 and Lebeda et al. 2007). In this regard, the development of interspecific bridge lines will greatly accelerate progress in *Cucurbita* breeding. For example, those created by Zhang et al. (2012b) among *C. maxima*, *C. moschata*, and *C. pepo* showed normal compatibility.

Cucurbita species are commonly used as rootstocks for grafting other cucurbit species, including cucumber, muskmelon and watermelon. This is due to their vigorous root systems, which are naturally tolerant of many abiotic stresses and also less susceptible to soilborne pathogens (Ferriol and Picó 2008; Lee et al. 2010; Pico et al. 2017). Grafted scions may additionally experience increased nutrient and water use efficiency, leading to higher yields. Hybrid rootstocks, such as those between *C. maxima* and *C. moschata*, are the most popular, and may also be used for grafting other *Cucurbita* species (Pico et al. 2017). Testing and development of different landraces and cultivars for use as rootstocks is ongoing.

11.5 *Momordica charantia*

Bitter gourd is a popular vegetable crop in Asia, as outlined in Section 2.4.8. Country-specific market demands for cultivars and/or landraces support a broad range of genetic diversity within cultivated gourds, and nearly 20 different market types are recognized (see Dhillon et al. 2017). However, the use of a small number of gynoecious inbred lines in the creation of commercial cultivars has led to reductions in genetic diversity (Dhillon et al. 2017). This narrow genetic base puts crops at risk of novel diseases, pathogen strains and/or pests, as well as changing environmental conditions. Apart from continuing to breed for earliness, yield and fruit characteristics, future work in crop improvement should also seek to develop more diverse cultivars.

Breeding cultivars resistant to problematic diseases is also desirable. According to Chia Tai Seed Co. data (John Sheedy, strategy expert consultation workshop, Thailand, Dec. 2019), the following viral diseases are highly relevant for gourds: CABYV, ToLCNDV and ZYMV. New cultivars should also carry resistance to two bacterial diseases, namely bacterial wilt and bitter gourd little leaf disease (*Phytoplasma*), as well as a number of fungal diseases: downy mildew, gummy stem blight and powdery mildew. By screening bitter gourd collections held by WorldVeg in Thailand, a source of resistance to powdery mildew was identified and used to breed resistant lines (Dhillon et al. 2015), and one accession resistant to the emerging disease CABYV was also found.

12 STORAGE, SEED HEALTH AND SEED LONGEVITY

12.1 Seed longevity

Ex situ conservation efforts largely rely on storing orthodox seeds (i.e., those that can survive drying or freezing for storage; Solberg et al. 2020) for long periods of time. Although storing large numbers of seeds is a cost-effective conservation strategy, it nonetheless becomes expensive, as there must be sufficient infrastructure and human resources, particularly for the regeneration of aging accessions. To limit costs (and the consumption of stored seed), seed health, seed storage conditions, viability monitoring and regeneration frequencies must be optimized (Li and Pritchard 2009). Overly frequent regeneration is unnecessary, but very infrequent regeneration creates the risk of unwanted viability selection (affecting the genetic integrity of the collection) or complete loss of viability and, ultimately, the accession (Fu 2017).

Despite the importance of seed longevity for *ex situ* conservation, basic knowledge is lacking for many crop species and their wild relatives (Colville and Pritchard 2019). Seed longevity may vary dramatically both among plant families and among species within a family (Walters et al. 2005; Colville and Pritchard 2019). For example, in a study of 42 species stored for 10 years under medium-term conditions (4 °C, 30–40% relative humidity [RH]), cucumber, watermelon and *Cucurbita* spp. seeds showed less than a 5% decline in viability, while muskmelon showed an 80% decline (Lee et al. 2013). Longevity may also vary among genotypes, populations and harvest years within a given species (Walters et al. 2010) and depending on the collection location and/or conditions (Walters et al. 2005). These factors remain poorly understood and add significant complexity to the task of making predictions for any given crop species. In the face of this lack of research, genebanks must still make decisions on regeneration frequency, though given the regener-

ation backlogs noted by many genebanks (see Section 13.1), the availability of funding and manual labor may largely dictate the schedule.

To assist in maintaining long-term seed survival, genebanks may utilize information gleaned from regular seed germination and/or viability testing to help determine when to regenerate stored accessions. According to the Cucurbitaceae strategy survey, genebanks vary considerably in how often they perform such tests, with most falling in the 5–25-year range, though one genebank (Empresa Hortaliças in Brazil) noted that testing was performed only very rarely. Note that as seed storage conditions may also affect seed longevity, the optimum testing schedule will also vary to some extent. For example, under the stringent conditions employed by the CGN genebank in the Netherlands, germination testing is only needed every 25 years. Where such conditions were not met, regular testing every 5–10 years is more common. Several genebanks noted that they adhered to standard protocols for testing, published by ISTA, but this was far from universal. In a few cases (e.g., the USDA in Geneva, New York), genebanks noted challenges with germination test backlogs and technical difficulties with germination tests themselves (e.g., moldy seeds).

As noted previously, seed longevity may depend on the specific storage conditions, in addition to intrinsic properties of the seeds themselves (and to interactions among these factors). The storage temperature, seed moisture content and the oxygen concentration may all influence longevity (Walters et al. 2010; Groot et al. 2012). Within limits, seed longevity increases as temperature and moisture content decrease, which is why seeds are typically dried and stored at low temperature for long-term storage (FAO 2013; van Treuren et al. 2013). However, there is some indication that current standard conditions for *ex situ* conservation

(–20 °C and ~15% RH) may be insufficient for the safe, long-term storage of a wide range of species (Colville and Pritchard 2019); therefore, enhancing seed lifespan represents an important avenue for future research. For example, some studies have suggested that drying seeds to extremely low moisture content (<6%), or "ultra-drying," may extend seed life in certain species (Singh et al. 2003), although other studies have shown detrimental effects of over-drying (Walters and Engels 1998; Ellis and Hong 2006). Additionally, seed aging is now known to be driven by oxidative processes, yet there is little research investigating the potential of seed storage under anoxic conditions. One recent study (Groot et al. 2015) showed that the presence of oxygen accelerated aging in celeriac and celery seeds (two crops with very short-lived seeds), and recommended that genebanks store dry seeds under anoxic conditions.

In light of the factors discussed above, the choice of seed storage containers may be critical for ensuring the long-term viability of accessions (Gómez-Campo 2006). Commonly used containers (e.g., glass flasks with twist- or screw-off lids, unsealed metal cans, plastic containers, foil bags, etc.) may fail to prevent the entry of water vapor, thus allowing seed moisture content to rise and seed viability to consequently decline. Inadequate containers are particularly problematic in cases where the RH level is high and/or not controlled, a fairly commonplace occurrence. For example, among the surveyed Cucurbitaceae genebanks, the RH of storage facilities was in the range of 5–60%, averaging 28%; in fact, a number of genebanks noted that RH was not controlled in any way. Seeds were stored in a number of container types (e.g., paper bags, aluminum foil packets, glass jars and a variety of plastic containers) of varying permeability, suggesting that seed longevity may be enhanced by upgrading storage containers in some genebanks. As an alternative to well-sealed glass containers (which are effective, but not always practical), new lightweight foil laminate packages offer excellent protection in high-humidity environments (Walters 2007). Container choice may be particularly important for genebanks situated in humid environments, such as those at lower altitudes, whereas genebanks at high altitudes have a natural advantage in terms of lower RH (the lower density of air at high altitudes reduces water vapor pressure).

12.1.1 *Momordica charantia*

Bitter gourd (*Momordica charantia*) seeds have been characterized as orthodox seeds that tolerate desiccation and can be stored at low temperatures to preserve their viability (Doijode 2001; Royal Botanical Gardens Kew 2020). However, this has not been the practical experience of many genebanks, which have faced significant challenges conserving *Momordica* germplasm (according to responses to the strategy survey). For example, unpublished work by the WorldVeg genebank has revealed extremely poor germination of *M. charantia* seeds after short cold-storage periods, in comparison with *Cucumis*, *Cucurbita* and *Lagenaria* seeds (Figure 12.1).

A second study by WorldVeg, with *M. charantia* seeds and the same storage period lengths, showed that low temperatures, particularly those used for long-term storage (–18 °C), are detrimental to the storage of bitter gourd seeds (Figure 12.2). Thus, the long-term storage of bitter gourd seeds in a freezer is not an option, making more frequent regeneration a necessity. Interestingly, the storage of bitter gourd seeds at subzero temperatures has been found to induce a secondary state of dormancy, which can be broken for some genotypes by a short heat treatment at 50 °C for 2–8 minutes (Bopper and Kruse 2018). Other studies have now confirmed that bitter gourd seeds are relatively short-lived compared to other orthodox seeds (Peter et al. 1998), and that viability may deteriorate rapidly after a year of storage in a refrigerator (4 °C) (Fonseka and Fonseka 2011). However, when seeds were stored at warmer temperatures above freezing (5 °C or 15 °C), germination rates remained above 40% after 10 years in storage (WorldVeg, unpublished data). Clearly, more research is needed to guide genebank managers in choosing the right conditions for the safe, long-term storage of *Momordica* accessions.
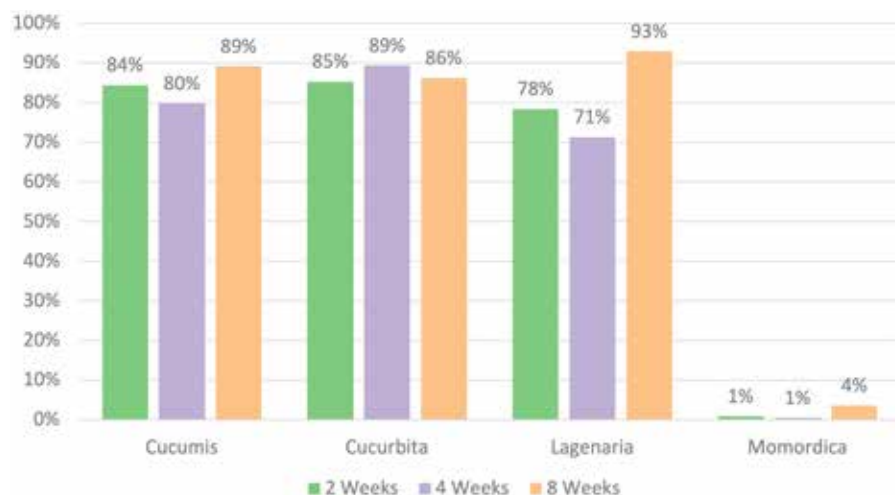
Figure 12.1 Germination of four cucurbit genera (*Cucumis, Cucurbita, Lagenaria and Momordica*) after varying storage periods at –18°C (WorldVeg 2020, unpublished data).

12.2 Storage conditions: survey results

Out of the 26 survey respondents, 24 (92%) indicated that the objective of their Cucurbitaceae collection is long-term conservation, 19 (73%) indicated that they conserve seeds in long-term storage at temperatures that meet FAO international standards (–18 °C ± 3 °C) (FAO 2013), and 84% stated that they have a genebank management system or written procedures for the storage and maintenance of germplasm. Of the genebanks that conserve material in long-term storage, 90% reported using aluminum foil bags as packing material. Survey results suggest that less attention is given to keeping RH within the range recommended by FAO international standards (15% ± 3%).

12.3 Seed health

As seeds are potential carriers of pests and pathogens, the distribution of seeds can risk introducing exotic pests and diseases into new geographic locations. This can result in severe crop damage and huge economic losses. Therefore, seedborne diseases in the Cucurbitaceae are a major concern in the movement of germplasm internationally, posing significant challenges for the USDA, WorldVeg and other genebanks that distribute seeds internationally (see Section 13.1). To ensure disease-free materials, importing countries often require that requested germplasm is accompanied by a plant health certificate. If seeds have not been tested for all the diseases and/or pests required by the importing country, the seeds cannot be sent. This results in lower accessibility of germplasm for research and breeding. Fifteen percent of survey respondents indicated that their collection is, to some extent, affected by plant disease that can restrict the distribution of germplasm (Figure 12.3).

As discussed in Section 11, a variety of pests and diseases affect cucurbit crops worldwide. For example, studies of plant pathogens in collections of bitter gourd and bottle gourd collected in Pakistan identified 15 genera and 29 species of fungi on bitter gourd (Sultana and Ghaffar 2007), and 22 genera and 45 species of plant pathogens on bottle gourd (Sultana and Ghaffar 2007). As it is difficult and extremely expensive for genebanks to invest in indexing, testing and certifying germplasm health against all possible diseases, one solution may be to designate regional third-party providers. This would require a donor agency to provide the necessary funds for germplasm

testing and certification. Furthermore, according to Kumar et al. (2021): "A strong case exists for positioning GHUs [germplasm health units] as part of a global network of phytosanitary hubs for research, diagnoses, and control of established and emerging pests as part of the One CGIAR program, set to operationalize in 2022."
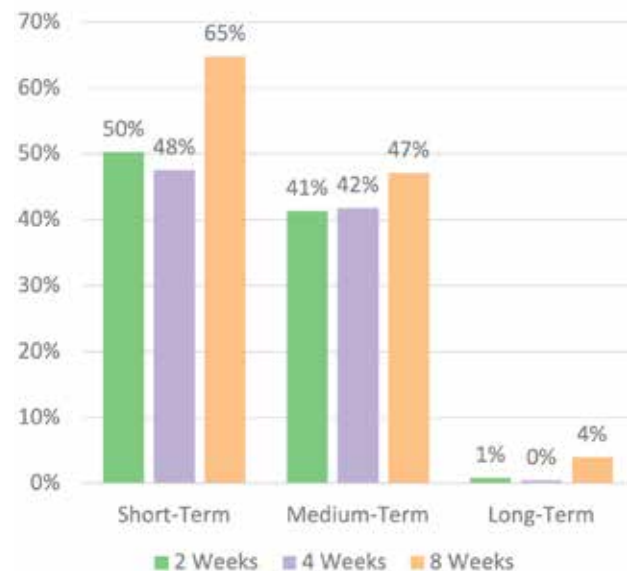
Figure 12.2 Germination of bitter gourd (*Momordica charantia*) seeds after storage for either two, four or eight weeks under different storage conditions. Short-term storage was at 15°C, while medium-term storage was at 5°C, and long-term storage at −18°C. (WorldVeg 2020, unpublished data).
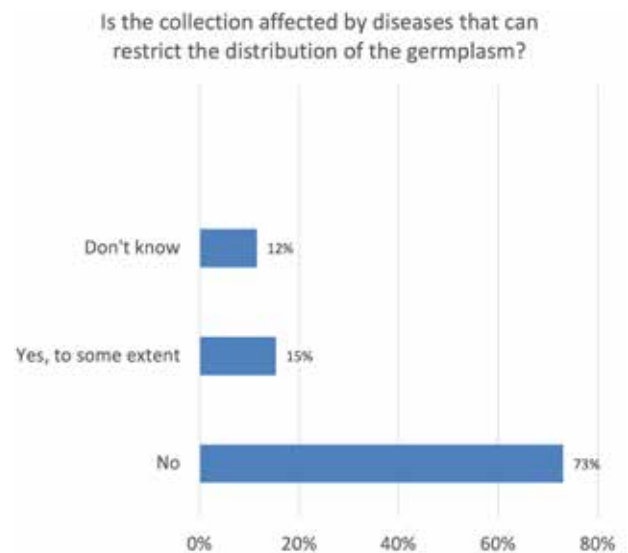
Figure 12.3 Extent to which diseases restrict genebanks' distribution of germplasm, according to responses to the strategy survey. n = 26.

Diversity of pumpkin and squash at Norwich Meadows Farm, USA. Source: L.M. Salazar/Crop Trust

13 IMPROVING CONSERVATION EFFICIENCY AND EFFECTIVENESS

The European Cooperative Programme for Crop Genetic Resources (ECPGR), a collaboration among nearly 40 European nations, was founded in 1980 to facilitate the long-term conservation and utilization of European plant genetic resources (PGR). In 2000, ECPGR initiated a Cucurbit Working Group, under the framework of the ECPGR Vegetables Network. At the first meeting in 2002, a plan of action was developed, including the following major tasks (Díez et al. 2002):

- the development of a European Central Cucurbit Database (ECCUDB), including not only passport, but also characterization and evaluation data;
- an assessment of current collection safety duplication status, with plans to consolidate safety duplicates at "base stores" with adequate facilities for long-term conservation;
- the establishment of standard guidelines for characterization and regeneration.

In a presentation at the meeting by Eva Křístková (Research Institute of Crop Production in Prague-Ruzyne, Czech Republic), additional goals for future international collaboration were discussed, especially the importance of the following: preserving landraces and old varieties, collecting expeditions to under-investigated regions (not just centers of origin), and detailed documentation and study of accessions. A progress meeting in 2010 celebrated the creation of the ECCUDB, progress in black-box safety duplication, and the development of minimum descriptor lists (for cucumber, muskmelon and watermelon).

Many of the points highlighted by the ECPGR Cucurbit Working Group meetings remain important today, as demonstrated during the expert consultation workshop for this strategy (Thailand, Dec. 2019) and by the Cucurbitaceae strategy survey. When asked what major limitations they face in managing their *ex situ* collections, roughly half of the surveyed genebanks

described insufficient funding and human resources as major impediments. Other limitations included inadequate infrastructure (space and/or facilities, equipment, etc.) and technical issues, such as the inherent complexity of seed regeneration in cucurbits and difficulties in preserving viable *Momordica* seeds. Furthermore, many genebanks noted backlogs in seed health or germination testing, and for the regeneration of accessions.

During the Cucurbitaceae strategy expert consultation workshop, working groups were formed to discuss priority conservation actions for major cucurbit crop groups (*Citrullus, Cucumis*, *Cucurbita* and gourds). The outcome of these discussions has been integrated into the following sections on regeneration, seed health and longevity, safety duplication, documentation/information systems, germplasm distribution/utilization, core collections and collaborations.

13.1 Solving regeneration issues

The periodic regeneration and multiplication of accessions stored in genebanks is essential both for maintaining seed viability and for replenishing seed stocks for distribution and safety duplication. However, regeneration can be costly, technically difficult and time consuming (Fu 2017), posing a significant challenge for long-term collection maintenance. As a result, many collections face a regeneration backlog (FAO 2010), putting much of their conserved diversity at risk of loss owing to declining seed viability.

As revealed in the strategy survey, Cucurbitaceae *ex situ* collections are no different; the vast majority of Cucurbitaceae species are stored as seeds (99%; n = 26 responding genebanks), and on average, nearly a quarter of accessions require urgent regeneration (24%; n = 22). Regeneration backlogs are common

(n = 19 out of 22 genebanks), and affect not only national genebanks, but also regional (e.g., Centro Agronomico Tropical de Investigaciòn y Enseñanza [CATIE], Costa Rica) (Figure 13.1) and international (e.g., WorldVeg) ones. A few genebanks have no backlog (e.g., CGN, Netherlands; the Leibniz Institute of Plant Genetics and Crop Plant Research [IPK], Gatersleben, Germany), but these represent a minority. In other cases (e.g., the Malawi Plant Genetic Resources Centre), the situation is much more dire, with all accessions requiring urgent regeneration.

Regeneration issues were also a common theme among surveyed genebanks when describing the major challenges they face with the management of their collections. In listing their top five major limitations, 15 out of 24 respondents highlighted regeneration as an issue, with several genebanks discussing regeneration exclusively. The high costs of regeneration, large spaces required and need for adequately trained personnel were common themes. Because Cucurbitaceae crops are outcrossing, regeneration is especially challenging, requiring special approaches to restrict pollen flow only to desired accessions (and to prevent pollen flow, e.g., from natural populations, in cases where related species are sympatric). Common regeneration techniques for outcrossing species include spatial or temporal isolation, caging and hand pollination. Spatial isolation often requires large distances, while hand pollination requires time-consuming manual labor. Genebanks also cited difficulties with low flowering levels in some accessions, insufficient numbers of male flowers (requiring chemical treatment, for example with silver nitrate), low seed multiplication ratios (necessitating more regeneration cycles) and disease control during regeneration. More generally, materials that are highly locally adapted (to a particular climate, latitude, photoperiod, etc.) may be difficult to grow or propagate in other regions; this is often the case particularly for CWRs. For CWRs, there may be additional challenges with seed dormancy and low seed viability.

Some of these issues could be overcome by building collaborations among genebanks, with those genebanks that have greater regeneration capacity (or more suitable environmental conditions) assisting those with regeneration backlogs. However, phytosanitary restrictions may limit the movement of germplasm internationally between collaborators. Another possibility is collaboration with private seed companies, a model that has been successful for CGN in Netherlands (Willem van Dooijeweert, personal communication). One downside is that private companies may be unwilling to perform the morphological characterization that is typically part of the regeneration process, or there may be issues with data sharing.

13.2 Filling research gaps in seed longevity and seed health

As discussed in Section 12, seed health and longevity are crucial issues for *ex situ* collections of Cucurbitaceae species, which are conserved and distributed as seeds. Seed longevity dictates the frequency of regeneration for accessions, but may be unpredictable, presenting a challenge to genebanks. Overly frequent viability testing and/or regeneration wastes resources, while the opposite risks accession loss. Further research is needed to better understand the factors that influence longevity and to develop storage recommendations that maximize longevity. Particular Cucurbitaceae species, such as those in the genus *Momordica*, also require further study, due to issues with relatively low seed longevity under orthodox conditions.

Seed dormancy is an important issue in bitter gourd and probably also in other *Momordica* species. Further research is required to understand seed behavior under 5 °C and –20 °C and to develop dormancy breaking protocols after short- and long-term storage. Because the seed of bitter gourd is relatively short lived, it is worth developing a cryo protocol to store germplasm of this species. Efforts in this regard have not been successful so far (Zhang et al. 1990).

Seedborne diseases in the Cucurbitaceae family are a major concern for the safe movement of germplasm across national borders. In their responses to the Cucurbitaceae strategy survey, several genebanks that distribute seed internationally (e.g., CGN, USDA and WorldVeg) described significant challenges to distribution as a result of issues associated with seed health. Testing and certifying germplasm health to meet phytosanitary requirements is costly and technically challenging. Stronger collaborations among genebanks within a given country or region may improve the

Figure 13.1 Regeneration of pumpkin accessions at CATIE. Source: World Vegetable Center

efficiency of germplasm certification. Another option would be to create designated third-party providers for each region, but this may be challenging owing to the idiosyncrasy of country-specific requirements.

The development of chemical or temperature seed treatments for disease-free cucurbit germplasm and research on their impact on seed longevity should be a priority for collaborative research on cucurbit conservation and germplasm exchange. Several seed treatments are being applied by seed companies including heating of pre-dried seeds of *Cucurbita* spp. and *Cucumis* spp. for 72 hours at 76°C to kill viruses and other pathogens (Maarten van Zonneveld, personal communication, expert consultation workshop Thailand, 11–13 Dec. 2019).

13.3 Safety duplication

Safety duplication off-site is essential for all accessions, as individual genebanks may suffer damage or losses of conserved materials. Under international genebank standards, such as those published by FAO (2013), genebanks should safety duplicate (or "back-up") any unique accessions (e.g., those held only by that particular genebank, or originally collected by the genebank). Ideally, duplicate accessions are held at two geographically distinct locations: one within the country (for easy accessibility) and one outside the country (to mitigate losses in case of a national disaster). A "black-box" approach is often taken to safety duplication, where the receiving genebank only stores the materials, and has no entitlement for use or distribution.

In their responses to the Cucurbitaceae strategy survey, 69% of genebanks (n = 26) reported having safety duplicated their cucurbit collections in another genebank, while 23% have not; the remaining 8% were unclear about the extent of safety duplication. However, in many cases where safety duplication had been performed, the safety duplicates were maintained within the same institution (at a separate location) and/or country. The *ex situ* collections of only seven genebanks were safety duplicated in the Svalbard Global Seed Vault. Thus, a lack of adequate safety duplication for Cucurbitaceae collections heightens the risk of genetic diversity losses. Although it is difficult to estimate how many of the accessions stored in these genebanks are unique, 58% reported that their collection is mostly unique and 42% that their collection is partly unique. These responses highlight the need for safety duplication of these collections.

In the survey, respondents identified a lack of financial resources and challenging quarantine regulations (and/or a lack of virus-free materials) as major

constraints to safety duplication in another country. Additionally, samples may need to be multiplied before duplication is possible; as discussed in Section 13.1, many genebanks have a regeneration backlog for their cucurbit collections.

The importance of safety duplication for threatened regional and international cucurbit collections (e.g., that of CATIE in Costa Rica) was also highlighted at the strategy expert consultation workshop. Apart from the Svalbard Global Seed Vault, genebanks can start to collaborate with each other to improve conservation and distribution of these collections. An example is the recent collaboration between the WorldVeg and CATIE genebanks to regenerate the CATIE *Cucurbita* spp. collection in multiple locations for long-term and mid-term storage and to make it available for distribution to the agricultural community.

13.4 Implementation of user-friendly documentation and information systems

The documentation of a genebank's germplasm collection, in an easily accessible, up-to-date database, is essential for collection management and utilization (FAO 2013). Moreover, the inclusion of passport, characterization and evaluation data add value for potential germplasm users, as it enables them to select the most suitable accessions. While many genebanks have developed their own data management systems, these often vary in quality (Fu 2017). This is also true in the case of genebanks with Cucurbitaceae collections, as discussed in Section 10. For example, not all genebanks have fully digitized their information systems to date (16% have yet to completely transition to an electronic system), and only 52% of genebanks provide online, publicly accessible accession information. Furthermore, survey respondents reported using a range of information management systems (Section 10), including online portals, dedicated software and general-purpose software (e.g., Microsoft Office).

The lack of appropriate documentation and information systems poses a significant challenge for the integration of Cucurbitaceae collections into the international PGR community, reducing opportunities for collaboration and the utilization of germplasm resources. One positive trend is the adoption of the GRIN-Global system (released in 2011 by Bioversity International, the Crop Trust and the USDA-ARS; Fu 2017) by a number of genebanks that have Cucurbitaceae collections (Section 11). GRIN-Global is a powerful, user-friendly, global information management system; once accession data are uploaded into GRIN-Global, it is simple to then share this information on Genesys (the Crop Trust's online platform for global PGR for food and agriculture). To facilitate germplasm documentation, those genebanks that lack effec-

tive systems could be assisted with the adoption of existing, proven systems, such as GRIN-Global. When passport data have been entered in Microsoft Excel (or Access) in a standard format (e.g., the FAO/Bioversity Multi-crop Passport Descriptors), the data may be easily uploaded to existing global information systems and databases (EURISCO, Genesys, WIEWS etc.; Willem van Dooijeweert, personal communication). Sharing accession-level information in widely used global databases will greatly enhance the utilization of germplasm resources.

A number of initiatives were discussed at the expert consultation workshop for the Cucurbitaceae strategy (Thailand, Dec. 2019). For example, to support vegetable science research, crop improvement and technological innovation in China, CAAS scientists are developing a vegetable resource platform. This platform has the following objectives: (i) provide an overview of the status of various collections; (ii) provide information on the availability and conservation of vegetable germplasm resources in China; and (iii) promote research on innovative uses of vegetable genetic resources (Haiping Wang, strategy expert consultation workshop, Thailand, 11-13 Dec. 2019).

Information on collections in Africa, the center of origin and diversity of *Citrullus* and maybe also *Momordica*, is currently lacking. Obtaining information on all existing collections (i.e., national, university and private collections) and collating this information in international databases is a priority. Once identified, high-value accessions might then be conserved and made available by the Southern African Development Community (SADC) Plant Genetic Resources Center (SPGRC; WIEWS Code = ZMB030). The N. I. Vavilov Research Institute (VIR) genebank in Russia may also represent an important source of information on and repository of *Citrullus* germplasm.

13.5 Key obstacles to germplasm distribution and utilization

As discussed in Section 9, the distribution of Cucurbitaceae germplasm is currently limited for many national genebanks, owing to a range of factors. In addition to a lack of funding, low seed numbers and poor germplasm health (see Section 13.2), challenges include poor documentation of collections, incomplete accession information, phytosanitary restrictions and policy issues.

As reviewed in Section 13.4, many national genebanks still lack accessible online information systems, posing a challenge for potential germplasm users searching for suitable materials. Additionally, as highlighted in the strategy expert consultation workshop (Thailand, Dec. 2019), users may face challenges when requesting this information (or germplasm) directly from the genebank: curators often do not respond in a timely manner and some fail to respond at all. Many genebanks work in isolation, and establish their own unique set of rules and regulations for germplasm distribution, adding further complexity to the process for potential users.

To date, characterization and evaluation remain a challenge for the majority of Cucurbitaceae collections (see Section 8), limiting the information available to potential users. The need to make obtaining such data a priority, and to make the data available in existing, publicly accessible databases, was also highlighted at the strategy expert consultation workshop. Evaluation can be particularly costly and difficult, as it often involves screening materials in different environments, for example, to determine suitability under changing climatic conditions. Several genebanks (e.g., CATIE in Costa Rica) intend to screen their collections with climate change adaptability in mind, if/when resources become available. There is also a need to develop and standardize descriptor lists for Cucurbitaceae crops. As reviewed in Section 8, there are several published lists of descriptors for many major crops (e.g., from the ECPGR Cucurbit Working Group, IPGRI, UPOV, USDA and WorldVeg GRSU); the use of different descriptors hampers efforts to compare germplasm collections.

Current phytosanitary restrictions also pose a major hurdle for international germplasm exchange, with more than a quarter of genebanks reporting inadequate procedures for phytosanitary certification. Testing at the regional level for seedborne diseases requires urgent funding; such testing would enable genebanks to distribute certified disease-free germplasm at affordable costs. To ameliorate the current situation, the USDA NPGS is also willing to provide germplasm to genebanks in other countries, if they are able to accept international germplasm shipments; this germplasm could then be incorporated into national or other programs. The development of standard seed treatments for disease-free germplasm can help to overcome this hurdle. Seed companies are already using heat treatments for seed of *Cucumis* and *Cucurbita* spp. Public organizations can learn from these experiences in order to test seed treatments for their effectiveness and impact on seed longevity.

Policy issues are also obstacles to germplasm distribution among countries. For example, many germplasm holders remain in doubt as to how to exchange materials under the regulations of the Nagoya Protocol. The Nagoya Protocol (Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization (ABS)), is a supplementary agreement to the Convention on Biological Diversity, and entered into force in October

2014. Its objective is the fair and equitable sharing of benefits arising from the utilization of genetic resources, to promote the conservation and sustainable use of biodiversity. As discussed at the strategy expert consultation workshop (Thailand, Dec. 2019), expanding the list of Annex I crops in the ITPGRFA to include the Cucurbitaceae would therefore facilitate germplasm exchange, as the ITPGRFA facilitates international distribution under an SMTA. Finally, national policies on germplasm exchange (not only nationally, but also regionally and internationally) vary tremendously, further complicating access to and sharing of Cucurbitaceae germplasm.

Some of the obstacles to distribution discussed here may be overcome through capacity-building measures, facility development and training. National genebanks should be engaged in germplasm collecting, conservation and characterization projects, initiated by international organizations such as Bioversity International, the Crop Trust, ECPGR and the USDA. It is important to work jointly with national genebanks to both characterize and evaluate their collections, and also to develop standardized policies for germplasm sharing.

13.6 Core collections

Conserving a broad diversity of crop genetic resources is essential for long-term conservation and agricultural sustainability. However, the large size of many *ex situ* collections is often an obstacle to their maintenance (e.g., safe storage and regeneration), characterization/evaluation and utilization, owing to the costs involved. This problem led to the development of the core collection approach (Frankel 1984).

A core collection is a subset of accessions of a collection selected to "include, with minimal redundancy, the genetic diversity of a crop species and its wild relatives" (Frankel 1984, p. 253).

A core collection should be representative of the entire collection, including species, subspecies and geographic regions, but also small enough (Frankel (1984) suggested 5–10% of the entire collection) to be easily managed and to facilitate its use (FAO 1996). There are many approaches to developing a core collection (van Hintum et al. 2000; Odong et al. 2013).

In the case of Cucurbitaceae crops, the creation of targeted core collections may be used to facilitate research and crop improvement. Two examples, both for cucumber (*Cucumis sativus*), may prove illustrative. Using genotyping-by-sequencing data, Wang et al. (2018) first genetically characterized the USDA cucumber collection, which comprises 1,314 domesticated and wild accessions. The USDA collection

includes cultivars, landraces and varieties collected worldwide, and is an important resource for pest and disease resistance long utilized by breeders. The core collection designed by Wang et al. (2018) included 354 accessions and represented 96% of the genetic variation present in the entire collection; it was also remarkably consistent with a previous core collection of 147 accessions designed using isozymes (Staub et al. 2002). To enhance utility for crop improvement, the final core collection included an additional 41 accessions (historical cultivars, breeding lines, etc.) of particular interest to breeders (n = 395 in total). Similarly, to enhance the use of cucumber germplasm, Lv et al. (2012) developed a core collection of 115 accessions for the joint collections of CAAS (China), CGN (Netherlands) and the USDA (n = 3,331 accessions in total) using SSR markers. A larger core collection (n = 251) is also under development by CAAS (Haiping Wang, strategy expert consultation workshop, Thailand, Dec. 2019).

13.7 Strengthening regional and international collaboration

There is a clear need to strengthen regional and international collaboration among genebanks and PGR scientists, given responses in the Cucurbitaceae strategy survey and feedback at the strategy expert consultation workshop (Thailand, Dec. 2019). At present, only a slim majority (54%) of genebanks that responded to the survey currently collaborate with other genebanks and/or public/private sector breeders on aspects of germplasm management (apart from safety duplication). These collaborations occurred with other genebanks, NGOs, private breeding or seed companies, and universities. Less than half of the surveyed genebanks (48%) participated in specific networks or project consortia, such as the ECPGR Cucurbits Working Group, the Consortium Research Platform on Agrobiodiversity (coordinated by the Indian Council of Agricultural Research [ICAR]) and the Cucurbit Coordinated Agricultural Project (CucCAP; coordinated by the USDA).

Collaborations, especially at the regional and international levels, would allow PGR scientists to work across geographic regions where crop genetic diversity is known to exist, allowing study of entire crop gene pools. Such collaborations could also result in joint publications, further disseminating information on crop diversity, genetic diversity and useful traits, in addition to providing recognition to participating contributors. From the point of view of the global Cucurbitaceae community, it is crucial to strengthen ties with some of the largest cucurbit collections (e.g., in China, Japan and Russia) and enhance germplasm sharing among regions (especially for *Cucurbita*).

To effect useful collaborations, uniform and stan-

dardized data management systems are needed (e.g., GRIN-Global; see Section 13.4) for ease of communication and data exchange (in global databases, such as Genesys, WIEWS, etc.). Additionally, scholarships for students to work at national, regional and international genebanks could not only provide needed support, but also potentially aid in the succession of skilled genebank staff. Finally, strengthening public–private collaborations (including those with the seed sector) may bring mutual benefits.

As discussed above, the ECPGR provides a good example of regional cooperation that may serve as a model for other regional/international networks. Since its inception, the ECPGR has worked to strengthen and consolidate PGR conservation in Europe, reducing the amount of duplication in conserved germplasm and conservation efforts, creating conservation standards and mandating coordination among participating countries and genebanks. Financed by the participating countries, the ECPGR is guided by a steering committee (composed of representatives from each country) and directed by an executive committee (elected by the steering committee). With a focus on crop genetic resource conservation, information management and capacity building, the ECPGR operates through a number of working groups, such as that developed for cucurbits (Maggioni and Thörn 2015).

As mentioned previously, the ECPGR has celebrated many successes, such as the creation of the European Search Catalogue for Plant Genetic Resources (EURISCO). An online catalogue of European *ex situ* PGRFA collections, EURISCO provides information on more than two million accessions (representing 6,719 genera and 45,131 species as of December 2020) hosted by over 400 institutes. Initially providing only passport data, EURISCO has recently begun including characterization and evaluation data. Any data gathered by EURISCO are also made available in Genesys.

In 2004, the ECPGR established the European Genebank Integrated System (AEGIS), an online "virtual" genebank for a select subset of European accessions (the selection criteria are set out on the AEGIS website). At the time of writing, 57,599 unique accessions are maintained at participating institutions under AEGIS, which mandates the technical standards for conservation (as part of the AEGIS quality management system). Membership is open to all European countries that are members of the ECPGR and willing to make PGRFA available under the ITPGRFA; materials listed on AEGIS can be requested from the host institute under an SMTA, with an explanatory note in the case of non-Annex I crops. As such, AEGIS represents an important contribution toward the implementation of the ITPGRFA (Engels and Maggioni 2018).
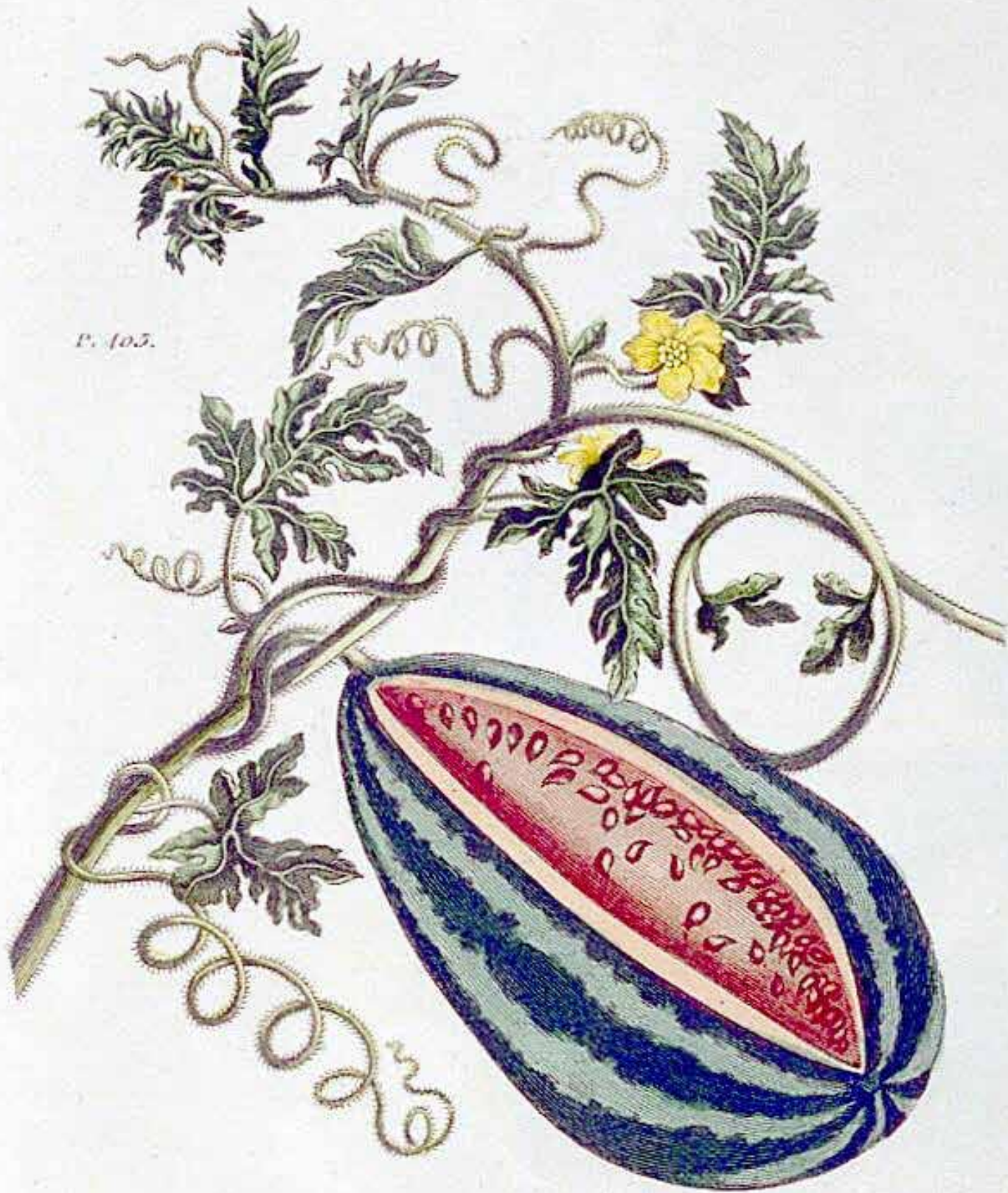
P. 105.

CUCURBITA CITRULLUS.

Water Melon.

Cucurbitra citrullus. 1820. Source: Thomas
Green/Wellcome Collection

14 A RATIONAL GLOBAL CONSERVATION STRATEGY FOR THE CUCURBITACEAE FAMILY

A global conservation strategy for Cucurbitaceae genetic resources should aim at improving the **comprehensive**, **secure**, **efficient** and **cost-effective conservation and use of** Cucurbitaceae plant genetic resources. Part of the strategy should also involve making germplasm and detailed accession-level information (ideally in centralized global databases such as Genesys) **easily accessible**.

14.1 Collecting threatened and missing genetic diversity

For many cucurbit crops, the existing gene pool may be limited with regard to both short-term and long-term needs of breeding programs, which continually face new diseases and insect pests. In the light of climate change, there is also a high demand for abiotic stress tolerance, for example, to heat, cold, drought, salt and acidity. Ideally, abiotic and biotic stress tolerance should be combined in new cultivars. To fill this diversity gap, it is important to address collection needs for wild relatives in the Americas and for landraces in primary regions of diversity (e.g., Mexico, sub-Saharan Africa), as well as other regions with unique diversity (e.g., Bangladesh, China, and Myanmar). Collections should be prioritized in extreme environments to capture abiotic stress tolerance and in areas with high pest and disease pressure to identify genotypes that present single or multiple resistance.

For *Citrullus*, Africa (the center of origin and diversity) is not well represented in existing collections, especially for wild taxa. For example, *C. ecirrhosus* and *C. rehmii* have fewer than 10 accessions each, and there are only two accessions of *C. naudinianus* in *ex situ* collections.

For *Cucumis sativus* (cucumber), major collecting expeditions should focus on African nations, as well as India, China and neighboring countries. India and China represent the centers of diversity for this species. Future explorations for *C. melo* (melon) germplasm should be directed toward eastern and southeastern Africa, and should secure *ex situ* germplasm of *C. picrocarpus*, muskmelon's closest CWR. Additional collecting in India is also desirable, as this particularly diverse region has been an important source of genes for disease and insect resistance, as well as other agronomic traits.

Among *Cucurbita* CWRs, *C. cordata*, *C. pedatifolia*, *C. radicans* and *C. x scabridifolia* are high priority for further collecting, followed by *C. digitata*, *C. foetidissima* and *C. palmata* (Khoury et al. 2020). For *Cucurbita argyrosperma* subsp. *argyrosperma*, further collecting of landraces in Central America and duplication of collections at risk should be a priority. For *C. moschata*, further germplasm should be collected from Colombia and from secondary centers of diversity (in Asia).

The large group comprising gourds (i.e., bitter gourd, bottle gourd, ivy gourd, pointed gourd, ridged gourd, snake gourd, spiny gourd, sponge gourd and wax gourd) requires additional collecting with a major focus on landraces from centers of origin and diversity; many landraces are threatened by the introduction of hybrid cultivars by seed companies, a process that recently began in many countries in South and Southeast Asia. Collecting should focus primarily on landraces in Bangladesh, Myanmar and Vietnam.

Collection of CWRs is also a priority for the most important gourds, including bottle gourd and bitter gourd. Collection of the wild relatives of bitter gourd and wild types of bitter gourd in sub-Saharan Africa is a priority to further broaden the genetic basis for breeding of this species and to understand its domestication history.

14.2 Global registry of *ex situ* Cucurbitaceae diversity

Documentation and data availability are key performance indicators for genebanks. Collection data should be made available online for easy access by potential users, enabling them to browse accessions and select those suitable for their purposes. However, several national genebanks still lack an adequate documentation and information system and, hence, are disconnected from the international PGR community and potential germplasm users. The Cucurbitaceae survey revealed that collection information is accessible online for 52% of genebanks, and is partially accessible online for 24% of genebanks; the remaining 24% of genebanks do not yet offer online access to collection information. These genebanks may require assistance to adopt an existing and proven documentation system, such as GRIN-Global. Once accession information is captured in a standard documentation

system, it can be easily shared with global databases (e.g., Genesys and WIEWS) to facilitate germplasm selection and distribution.

A large proportion of Cucurbitaceae collections also lack accession information on biological status, creating difficulties for assessments of global holdings. This applies to all three major genera conserved *ex situ*: *Cucurbita* (42.2%), *Citrullus* (40%) and *Cucumis* (28%). This information should be required when entering passport data for a new accession and should be included when genebanks share their data on open databases such as Genesys and WIEWS.

There are also taxonomic issues that need to be resolved. For example, the proportion of accessions with unidentified *Cucurbita* taxa in Genesys (10.4%) and WIEWS (13%) is rather high. The identification of unknown taxa may be performed during regeneration, but national genebanks may need taxonomic support for correct species identification.

Building on the European Cucurbits Database (ECCUDB), the Cucurbitaceae community should develop a global registry of collections conserved *ex situ*. A first step would be the sharing and verification of passport data, ideally with images of each accession, followed by the integration of characterization data and, where available, evaluation data. For such an effort to succeed, it would be important to have all major Cucurbitaceae holding institutes participate, including those not yet reporting on WIEWS and/or Genesys. Participation by major players such as CAAS (China), NBPGR (India) and VIR (Russia) would be critical; other useful participants would be countries such as Argentina, Mexico and Uzbekistan, where significant genetic diversity is found, and African genebanks such as the regional genebank of WorldVeg in Tanzania and the SADC Plant Genetic Resources Network, which are located in a major region of cucurbit diversity.

Once a reliable global registry of *ex situ* Cucurbitaceae diversity has been created, a virtual global core collection of unique accessions could be assembled, following the example of the AEGIS project in Europe. In the creation of the global core collection, entry requirements would need to be agreed upon, as well as common standards for maintaining accessions in the virtual collection.

14.3 Safeguarding Cucurbitaceae collections and improving use

Many Cucurbitaceae accessions are at risk owing to issues with seed longevity, regeneration backlogs and poor safety duplication. There are clear research gaps regarding the seed longevity of diverse cucurbit genera (see Section 12), which is a cause of uncer-

tainty for genebanks when deciding on schedules for viability testing and accession regeneration. In particular, the long-term conservation of *Momordica* species has suffered, owing to incorrect information and insufficient knowledge on storage temperature. For all cucurbit genera, the long-term storage conditions necessary to maintain seed viability for 25 years require further study, as recommended by CGN. Extending the safe storage period would significantly reduce conservation costs for cucurbit accessions.

Many genebanks are facing regeneration backlogs for their cucurbit collections, with 24% of accessions requiring urgent regeneration (see Section 13.1). As Cucurbitaceae crops and CWRs are generally outcrossing, regeneration can be costly, as it is heavily dependent on manual labor. Regeneration may also fail for exotic germplasm that relies on particular conditions for setting seed (or to flower, in the case of photoperiodism). Poor seed longevity in storage (common for CWRs) may also contribute to regeneration backlogs, as more frequent regeneration is needed. Such backlogs threaten the safety of conserved accessions, and limit the materials that may be distributed to users. Potential solutions (discussed in Section 13) involve greater collaboration among genebanks (with some specializing in regeneration) or with private industry, but neither approach is without its drawbacks.

Only 69% of genebanks have fully safety duplicated their cucurbit collections (see Section 13.3), and most collections are not backed up outside the host country, as recommended by international genebank standards (FAO 2013). To safeguard unique landraces and CWRs held by national genebanks (and not yet safety duplicated), a regional approach is advised, using the WorldVeg regional genebank in Tanzania (In 2022 this genebank will be upgraded to become the Pan-African Vegetable Genebank), the SADC Plant Genetic Resources Network in Southern Africa, the USDA NPGS for the Americas, members of AEGIS for Europe, and WorldVeg for Asia and Oceania. These genebanks could store accessions under a black-box agreement, and replace materials lost from national collections when needed (following all phytosanitary requirements). This would allow national programs to reduce their investment in duplication. However, any single conservation site may be lost; therefore, to obtain a higher level of security, accessions should be duplicated at two locations: one at another genebank, ideally located in another country, and one at the Global Seed Vault in Svalbard, Norway.

To improve the utilization of currently available accessions, it is necessary to create standardized descriptor lists for each Cucurbitaceae crop and address phytosanitary constraints to distribution. To date, UPOV has

developed descriptors for bitter gourd, bottle gourd, cucumber, muskmelon, watermelon and three species of squash (see Section 8). The ECPGR Cucurbit Working Group has developed minimum descriptor lists for not only *Cucurbita* spp., but also cucumber, muskmelon and watermelon. The USDA NPGS has its own descriptor lists for all listed species (as well as chayote and *Trichosanthes* spp.), and WorldVeg has comprehensive descriptor lists for the same species adapted from the National Plant Genetic Resources Laboratory (NPGRL) in the Philippines. Many of the descriptor lists are similar; nonetheless, it would be more useful to have a universal descriptor list for each crop, similar to those published by IBPGR/IPGRI/Bioversity International for melon.

Seedborne diseases represent a challenge for international distribution, and currently limit seed sharing by CGN, the USDA NPGS and WorldVeg. As it is technically difficult and extremely expensive to test and certify germplasm health, regional centers might serve as designated third-party providers of germplasm certification services. Regional centers should be genebanks such as EURISCO/AEGIS, SADC-PGRC, USDA NPGS and WorldVeg that have a clear mandate for international exchange. This would require donor agency support. The development of chemical or temperature seed treatments for disease-free cucurbit germplasm and research on their impact on seed longevity should be a priority for collaborative research on cucurbit conservation and germplasm exchange.

14.4 Policy issues

Current Cucurbitaceae collections are held by a broad range of institutions, including national programs, state or regional research and extension programs, universities, international centers and other entities. These vary considerably in the types of materials that they maintain and in their protocols for conservation, viability monitoring and distribution. As Cucurbitaceae genetic resources are not included in Annex I of the ITPGRFA, and recent intergovernmental negotiations have failed to expand the list of Annex I crops, national genebanks and other germplasm holders are, to some degree, free to determine independently what is in their best interest; any germplasm exchanges are commonly governed by the Nagoya Protocol.

All international CGIAR genebanks and the regional genebank CATIE (Costa Rica) have signed Article 15 agreements with the Governing Body of the ITPGRFA, and are sharing their germplasm under an SMTA. However, ILRI and ICARDA, the only CGIAR genebanks that conserve Cucurbitaceae germplasm, hold only a handful of accessions. Hence, CATIE is the only major Cucurbitaceae-holding institute that is a contracting party to the Governing Body of the ITPGRFA. WorldVeg, an international nonprofit research and development institute that is loosely associated with the CGIAR, holds a significant international collection of cucurbit genetic resources, but is still in communication with the Governing Body of the ITPGRFA about signing the Article 15 agreement. However, WorldVeg strictly follows its rules and regulations, and distributes germplasm under an SMTA. Several European genebanks, such as CGN, IPK and NordGen, also share materials under an SMTA, but most genebanks are obliged to distribute germplasm under the Nagoya Protocol.

An interesting approach has been implemented by the European Genebank Integrated System (AEGIS) (see Section 13.8): to use an SMTA under the ITPGRFA to share materials even from crops that are not listed in Annex I. This approach could ameliorate key obstacles to germplasm exchange, which currently limit the distribution of Cucurbitaceae crops, according to participants in the strategy expert consultation workshop (Thailand, Dec. 2019).

14.5 Implementation and funding

Formal discussions are required at the international level among leading national, regional and international genebanks. With consensus, select genebanks located in Africa (WorldVeg and SADC-PGRC), the Americas (USDA NPGS), Europe (EURISCO/AEGIS) and Asia (WorldVeg) may assume a special mandate for the long-term conservation and safety duplication of unique cucurbit accessions from national programs. The mandate would include the international exchange of cucurbit germplasm, with distribution occurring in strict compliance with phytosanitary regulations.

Many national programs struggle with safely conserving and regenerating their Cucurbitaceae collections; characterizing and evaluating accessions in appropriate environments; and managing accession information systematically and accurately, for the benefit of germplasm users, growers and consumers. The most urgent challenge for long-term preservation of valuable germplasm appears to be that some national programs are at risk of permanently losing accessions, particularly in centers of origin and diversity for Cucurbitaceae crops. Support should be provided as a priority to programs that meet standard conservation guidelines and/or those that have a track record of germplasm exchange at the national, regional or even international level. This approach would both reduce the risk of genetic diversity losses from at-risk genebanks and support the safety duplication of these materials in select regional or international genebanks. Such a strategy will go a long way toward preventing the serious erosion of cucurbit genetic resources.

Melon. 1575. Source: Jacques Lemoyne de Morgues/Victoria and Albert Museum
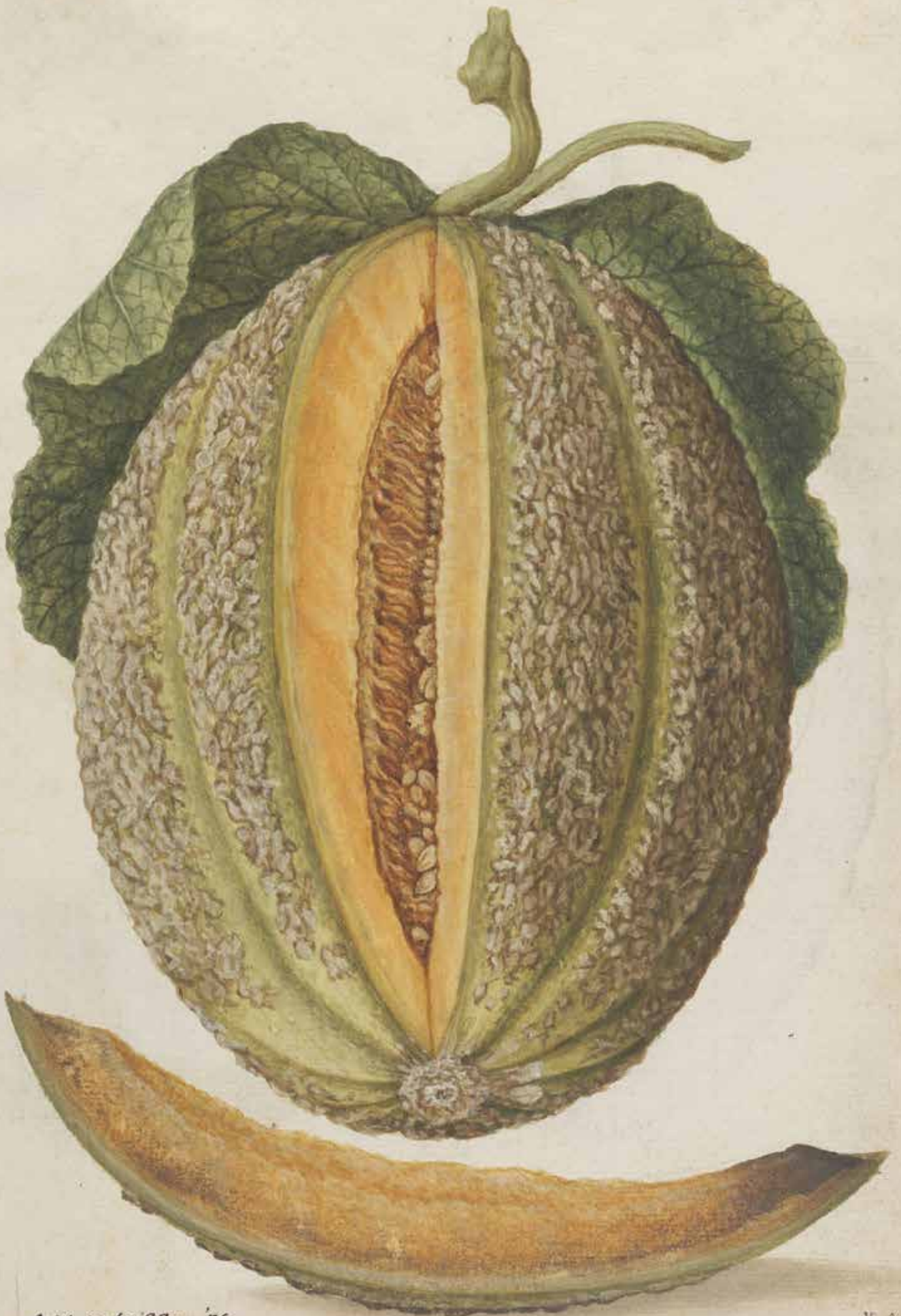
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APPENDIX I. AGENDA OF PROJECT KICK-OFF MEETING

14–15 October 2019, Crop Trust offices, Platz der Vereinten Nationen 7, Bonn, Germany

Breathing New Life into the Global Crop Conservation Strategies: Providing an Evidence Base for the Global System of *Ex Situ* Conservation of Crop Diversity

Sunday, 13 October 2019
Participants arrive

Monday, 14 October 2019

Time	Item	Lead
9:00 - 9:30	Welcome and round of introductions	HD, all
9:30 - 10:15	Introduction, goals, timeline of the Project: "Breathing New Life into the Global Crop Conservation Strategies: Providing an Evidence Base for the Global System of *Ex Situ* Conservation of Crop Diversity"	HD
10:15 - 10:45	Treaty context and the "meta-strategy"	Alvaro Toledo
10:45 - 11:15	Tea & Coffee break	
11:15 - 11:45	The 'strategy development process' in the past: Developing a global Conservation Strategy of Cassava	Clair Hershey
11:45 - 12:30	Diversity Trees as a key tool for conservation strategies to quantify crop diversity	PG
12:30 - 13:30	Lunch	
13:30 - 14:00	Overview of existing strategies, diversity trees completed and under development etc.	HD, PG
14:00 - 15:00	Data sources for updating strategies	Stephan Weise, Bonnie Furman, PG, HD, open discussion
15:00 - 15:30	Tea & Coffee break - Group picture	
15:15 - 16:30	What crops/crop groups to focus on for development of new strategies updating existing strategies	Discussion moderated by LG
16:30 - 17:00	Overview of the "meta-strategy"	Colin Khoury (via video-link)
18:00	Dinner at 'Im Stiefel' (center of Bonn)	all

Tuesday, 15 October 2019

Time	Item	Lead
9:00 - 9:15	Recap from Day 1	HD
9:15 - 9:45	Stakeholder mapping: Who will use the strategies and how?	HD
9:45 - 10:30	Discussion on scope, priorities and what key elements should be present in every strategy	Moderated by HD
10:30 - 11:00	Tea & Coffee break	
11:00 - 12:00	How to create 'living documents' that are actively used stakeholders?	Moderated by LG
12:00 - 13:00	Lunch	
13:00 - 13:30	Beyond the project: How to embed updated and new strategies into Treaty processes as guides for global conservation efforts post 2022?	Discussion moderated by AT
13:30 - 14:00	Synthesis of outcomes of all discussion sessions	LG, HD, PG, all
14:00 - 14:30	Tea & Coffee break	
14:30 - 15:00	Formation of informal 'advisory group' for project	HD
15:00 - 15:30	Meeting closing and wrap-up	HD
15:30	Some participants depart	
18:00	Dinner	

Wednesday, 16 October 2019
Participants depart

APPENDIX II. LIST OF PARTICIPANTS AT BONN WORKSHOP

14–15 October 2019

Alvaro Toledo (participated via video-link, ITPGRFA, Italy)

Andreas Ebert (independent, Germany)

Bonnie Furman (FAO, Italy)

Clair Hershey (independent, USA)

Colin Koury (participated via video-link, USDA ARS & CIAT, USA)

Fernando Ortega (INIA, Chile)

Frederike Zeibig (University of Bonn and Crop Trust)

Gayle Volk (USDA ARS, USA)

Gisella Cruz (could not attend in person but provided written input, Oxfam Novib, The Netherlands)

Hannah Jaenicke (representing WorldVeg, Germany)

Hannes Dempewolf (Crop Trust)

Yulia Ukhatova (VIR, Russia)

Imke Thormann (BLE, Germany)

Jan Engels (independent, formerly Bioversity International, Italy)

Lorenzo Maggioni (ECPGR, Italy)

Luigi Guarino (Crop Trust)

Michael Abberton (IITA, Nigeria)

Paul Smith (BGCI, UK)

Peter Giovannini (Crop Trust)

Sandy Knapp (NHM, UK)

Sherry Jacob (NBPGR, India)

Stefano Diulgheroff (participated via video-link, FAO, Ghana)

Stephan Weise (IPK, Germany)

APPENDIX III. CUCURBITACEAE STRATEGY SURVEY RESPONDENTS

Respon-dent	Response Date	Acronym	WIEWS Inst code	Location	Country	Contact Name
Instituto de Investigaciones Agropecuarias; www.inia.cl/recursosgeneticos/						
1	Oct 28 2019 01:35 PM	INIA Intihuasi	CHL028	Santiago, Region IV	Chile	Erika Salazar
Centro Agronomico Tropical de Investigaciòn y Enseñanza; www.catie.ac.cr						
2	Oct 25 2019 09:03 PM	CATIE	CRI085	Turrialba, Cartago	Costa Rica	Daniel Fernàndez
Universitat Politècnica de València; http://www.upv.es						
3	Oct 27 2019 10:29 PM	BGUPV	ESP026	Valencia	Spain	José Vicente Valcárcel; María José Díez
Agroscope; www.agroscope.ch						
4	Oct 29 2019 03:26 PM	Agroscope Changins	CHE001	Nyon 1	Switzerland	Beate Schierscher-Viret
Tropical Pesticides Research Institute - National Plant Genetic Resources Centre; www.tpti.go.tz						
5	Oct 29 2019 11:05 AM	NPGRC	TZA016	Arusha	Tanzania	William Chrispo Hamisy
Southern Regional Plant Introduction Station, University of Georgia, USDA/ARS/PGRU						
6	Oct 30 2019 01:13 PM	S9	USA016	Griffin, Georgia	USA	Robert Jarret
North Central Regional Plant Introduction Station - USDA; https://www.ars.usda.gov/midwest-area/ames/plant-introduction-research/						
7	Oct 28 2019 06:39 PM	NC7	USA020	Ames, Iowa	USA	Kathleen Reitsma
Seed Savers Exchange; www.seedsavers.org						
8	Oct 25 2019 02:31 PM	SSE	USA974	Decorah, Iowa	USA	Philip Kauth
Research Institute of Plant Industry						
9	Oct 30 2019 08:07 AM	UzRIPI	UZB006	Tashkent region	Uzbekistan	Dr. Safar Alikulov, Research Director of UzRIPI; Dr. Fayzulla Abdullaev, Head of Genebank
USDA National Plant Germplasm System, Plant Genetic Resources Unit; https://npgsweb.ars-grin.gov/gringlobal/search.aspx?						
10	Nov. 14 2019 at 21:22:14	NE9	USA003	Geneva, NY	USA	Joanne Labate
Empresa Hortaliças; https://www.embrapa.br/hortalicas						
11	Nov. 14 2019 at 20:38:57	CNPH	BRA012	70275-970 Brasilia, DF	Brazil	Geovani Bernardo Amaro
Crop Research Institute; https://www.vurv.cz/index.php?p=index&site=default_en						
12	Nov. 14 2019 at 09:12:13	CRI	CZE122	Prague	Czech Republic	Ivana Dolezalova
The Plant Breeding and Acclimatization Institute (IHAR) - National Research Institute; https://www.ihar.edu.pl/						
13	Nov. 12 2019 at 10:15:05	IHAR	POL003	Blonie 05-870	Poland	Grzegorz Bartoszewski
Malawi Plant Genetic Resources Centre; Chitedze Research Station						
14	Nov. 12 2019 at 00:41:18	MPGRC	MWI041	Lilongwe	Malawi	Lawrent Pungulani, PhD
Nordic Genetic Resource Center; https://www.nordgen.org						
15	Nov. 11 2019 at 16:58:20	NORDGEN	SWE054	Alnarp	Sweden	Annette Hägnefelt

Respon-dent	Response Date	Acronym	WIEWS Inst code	Location	Country	Contact Name
Centre for Genetic Resources the Netherlands (CGN); http//www.wur.nl/cgn						
16	Nov. 11 2019 at 14:37:21	CGN	NLD037	Wageningen	Netherlands	Willem van Dooijeweert
EMBRAPA; www.embrapa.br						
17	Nov. 08 2019 at 22:12:52	CENARGEN	BRA003	Brasilia, DF	Brazil	Rosa Lía Barbieri
IPK Gatersleben; https://www.ipk-gatersleben.de/						
18	Nov. 08 2019 at 13:46:52	IPK	DEU146	Seeland, OT Gatersleben	Germany	Britta Ruckwied
Instituto Nacional de Investigação Agrária e Veterinária- Banco Português de Germoplasma Vegetal; www.iniav.pt						
19	Nov. 07 2019 at 18:22:05	BPGV-DRAEDM	POR001	S. Pedro de Merelim	Portugal	Filomena Rocha
National Agriculture and Food Research Organization (NARO) Institute of Vegetable and Floriculture Science						
20	Nov. 03 2019 at 15:03:47	NIVOT	JPN005	Kusawa 360, Ano, Tsu, Mie 514-2392	Japan	Yoichi Kawazu
Institute of Vegetables and Flowers; http://ivf.caas.cn/						
21	Nov 18 2019 at 01:13 PM	ICS-CAAS	CHN001	12 Zhonguancun Nandajie Haidian District, Beijing	China	Haiping Wang
Brazilian Agricultural Research Corporation; https://www.embrapa.br/en/semiarido						
22	Nov 18 2019 at 17:23:54	CPATSA	BRA017	Petrolina, Pernambuco	Brazil	Rita de Cássia Souza Dias
World Vegetable Center; https://avrdc.org/						
23	Nov. 21 2019 at 03:45:16	AVRDC	TWN001	Shanhua, Tainan	Taiwan	Yung-kuang Huang
ICAR-National Bureau of PlantGenetic Resources; www.nbpgr.ernet.in						
24	Nov. 20 2019 at 11:21:17	NBPGR	IND001	Pusa Campus, New Delhi	India	Chithra Devi Pandey
National Arid Land Plant Genetic Resources Unit (National Plant Germplasm System, USDA-ARS); https://www.ars.usda.gov/pacific-west-area/davis-ca/natl-clonal-germplasm-rep-tree-fruit-nut-crops-grapes/docs/national-arid-land-plant-genetic-repository-parlier-ca/						
25	Nov. 22 2019 at 01:28:50	PARL	USA955	Parlier, California	USA	Claire Heinitz
Suceava Genebank; www.svgenebank.ro						
26	Nov. 22 2019 at 09:11:22	BRGV	ROM007	Suceava	Romania	Danela Murariu
N. I. Vavilov All-Russian Institute of Plant Genetic Resources (VIR); www.vir.nw.ru						
27	Nov. 25 2019 at 11:20:54	VIR	RUS001	St. Petersburg 190000	Russia	Tatiana Piskunova
Instituto Nacional de Tecnología Agropecuaria; www.inta.gob.ar						
28	Nov. 25 2019 at 16:00:19	INTA-EEALC	ARG013	La Consulta, Mendoza	Argentina	Leonardo Togno

APPENDIX IV. LIST OF PARTICIPANTS AT THE STRATEGY EXPERT CONSULTATION WORKSHOP IN THAILAND

11–13 December 2019

No.	Country	Name	Organization
1	Bangladesh	Abu Masud	BARI
2	Spain	Antonio Monforte	CSIC
3	Germany	Andreas Ebert	Crop Trust
4	Costa Rica	Carlos Cordero	CATIE
5	Benin	Carlos Houdegbé	University of KwaZulu-Natal (UKZN)
6	USA	Colin Khoury	USDA
7	India	Chithra Pandey	NBPGR
8	Thailand	Chamnong Somkul	TVRC-Kasetsart University
9	Thailand	Delphine Larrousse	WorldVeg
10	Spain	Fátima Tena Fernández	RijkZwaan
11	Germany	Hannes Dempewolf	Crop Trust
12	Bejing China	Haiping Wang	CAAS
13	Thailand	John Sheedy	APSA/ Chia Tai
14	Taiwan	Maarten van Zonneveld	WorldVeg
15	Thailand	Marylin Belramino	East West Seed
16	Thailand	Narinder Dhillon	WorldVeg
17	Thailand	Saowalak Ruangnam	East West Seed
18	Netherlands	Willem van Dooijeweert	CGN
19	Mexico	Xitlali Aguirre Dugua	Universidad Nacional Autonoma de Mexico

APPENDIX V. PROGRAM FOR THE STRATEGY EXPERT CONSULTATION WORKSHOP IN THAILAND

11–13 December 2019

Expert consultation workshop: Global Conservation Strategy for crops in the Cucurbitaceae family

Program

Organizers: Crop Trust and the Word Vegetable Center
Location workshop: Kasetsart University, WorldVeg - Kamphaeng Saen Campus
Location hotel: Mida Hotel

Date and time	Activity	Speaker
December 11th		
08:00 am – 08:30 am	Bus transport from Hotel to WorldVeg- Kampheng Saen campus	
08:30 am – 08:40 am	Opening, Goals & Objectives of the meeting	Delphine Larousse
08:40 am – 09:00 am	Scope of Global Crop Conservation Strategies	Hannes Dempewolf
09:00 am – 10:00 am	Round of introduction of participants	2 minutes each
10:00 am – 10:15 am	Coffee break	
10:15 am – 11:00 am	Background on Cucurbitaceae crops (number of crops, uses, taxonomy, centers of origin/diversity etc.)	Andreas Ebert
11:00 am – 12:00 pm	Presentation of survey results and preliminary analysis	Andreas Ebert
12:00 pm – 13:00 pm	Lunch	
13:00 pm – 13:15 pm	Conservation status of Cucurbitaceae crops in China	Haiping Wang
13:15 pm – 13:30 pm	Conservation status of Cucurbitaceae crops in India	Chithra Pandey
13:30 pm – 13:45 pm	Conservation status of Cucurbitaceae crops in Mexico	Xitlali Aguirre Dugua
13:45 pm – 14:00 pm	Conservation status of Cucurbitaceae crops in Brazil	Nuno Madeira
14:00 pm – 15:00 pm	Discussion of current status of conservation, diversity tree, gaps and data availability	Plenary
15:00 pm – 15:30 pm	Coffee break	
15:30 am – 16:30 am	Discussion of vulnerability and threats to genetic diversity	Plenary
16:30 pm – 16:35 pm	Closure	Maarten van Zonneveld
16:40 pm – 17:10 pm	Bus transport from WorldVeg- Kamphaeng Saen campus to hotel	
18:30 pm	Pick up from Hotel to the Restaurant (Welcome Dinner)	
December 12th		
08:00 am – 08:30 am	Bus transport from hotel to WorldVeg- Kamphaeng Saen campus	
08:30 am – 09:30 am	Status and future priorities for germplasm screening, characterization and evaluation	Antonio Monforte
09:30 am – 10:00 am	'Use perspective', Update from WorldVeg cucurbit breeding program	Narinder Dhillon
10:00 am – 10:10 am	'Use perspective', Update from East West Seed	Marilyn Belarmino and Saowalak Ruangnam
10:10 am – 10:20 am	'Use perspective', Update from Rijk Zwaan	Fatima Tena Fernandez

Date and time	Activity	Speaker
10:20 am – 10:30 am	'Use perspective', Update from Chai Tai APSA	John Sheedy
10:30 am – 10:45 am	Coffee break	
10:45 pm – 11:30 pm	Discussion on research gaps in screening, characterization, evaluation, and conservation	Plenary
11:30 pm – 12:00 pm	Discussion on availability, accessibility and policy issues	Plenary
12:00 pm – 13:00 pm	Lunch	
13:00 pm – 15:00 pm	Development and presentation of priority conservation actions per cucurbit crop group	Working groups
15:00 pm – 15:30 pm	Coffee break	
15:30 pm – 16:30 pm	Discussion and summary of Global Conservation priorities for Cucurbitaceae crops	Plenary
16:30 pm – 16:35 pm	Closure	Maarten van Zonneveld
16:40 pm – 17:10 pm	Bus transport from WorldVeg- Kamphaeng Saen campus to Hotel	
18:30 pm	Dinner at Hotel	
December 13th		
08:00 am – 08:30 am	Pick up from Hotel to WorldVeg- Kamphaeng Saen campus	
08:30 am - 10:30 am	WorldVeg field visit	
10:30 am - 10:45 am	coffee breaks in the field	
10:45 am - 11:45 am	visit to the Tropical Vegetable Research Center (TVRC), Kasetsart University	
12:00 pm - 13:00 pm	Lunch	
13:00 pm –14:00 pm	Pick up from WorldVeg- Kamphaeng Saen campus to East West Seed	
14:00 pm - 16:00 pm	Visit East West Seed, Supanburi province	
16:00 pm –17:00 pm	Transport back to the Hotel	
18:30 pm	Dinner at Hotel	

APPENDIX VI. CUCURBITACEAE STRATEGY ONLINE SURVEY FORM

CROP TRUST   **World Vegetable Center**

Conservation strategy of crops of the Cucurbitaceae family

INTRODUCTION

The Global Crop Diversity Trust (Crop Trust) is supporting efforts to develop strategies for the more efficient and effective conservation of crop diversity, particularly in *ex situ* collections. The Crop Trust in partnership with the World Vegetable Center (WorldVeg) has commissioned an independent external consultant to coordinate the development of a conservation strategy for crops of the Cucurbitaceae family. This questionnaire has been developed in order to seek the advice and input of representatives of relevant stakeholders around the world in the   development of the conservation strategy. In particular, the questionnaire seeks to assess the status of the conservation of crop genetic resources of the Cucurbitaceae family throughout the world.

WorldVeg and the Crop Trust are keen to have your active participation in the development of the conservation strategy of crops of the Cucurbitaceae family and will be pleased to keep you informed on its progress and consult you during the development until completion. After completion, the strategy will be shared with you.

Please complete the survey by November 16 2019.

If you have any questions about this questionnaire or about the proposed strategy in general, please contact maarten.vanzonneveld@worldveg.org and/or ebert.andreas6@gmail.com.

* 1. Does your institute maintain an *ex situ* collection of crops of the Cucurbitaceae family?
Yes | No

Question concerning institutes NOT maintaining ex situ collection

2. If your institute does NOT maintain an *ex situ* collection of Cucurbitaceae, please indicate to the best of your knowledge, the following
Current conservation activities
Institute focal person to contact for further details
Plans for any ex situ conservation
Any other information

3. Please add any further comments you may have.

Contact Information

4. Organization maintaining the Cucurbitaceae collection
Name of Organization
Website
Address
City/Town
State/Province
ZIP/Postal Code
Country

5. Type of organization
Governmental organization | University | Private organization | Other (please specify)

6. Curator of the Cucurbitaceae collection
Name
Email Address
Phone Number

7. Name of respondent to this survey – if not as above
Name
Function/Job Title
Email Address
Phone Number

The Cucurbitaceae Collection

8. What is the objective of the collection? (select all applicable)
long-term conservation | working collection | breeding collection
Other (please specify)

9. Basic Information
Year of establishment
Total number of species today
Total number of accessions today
Total number of accessions currently available for distribution

10. Number of <u>species</u> today as per the following major genera:
(a) Citrullus
(b) Cucumis
(c) Cucurbita
(d) Benincasa
(e) Momordica
(f) Lagenaria

11.Number of accessions today as per the following major genera:
(a) Citrullus
(b) Cucumis
(c) Cucurbita
(d) Benincasa
(e) Momordica
(f) Lagenaria

12. What would you consider to be the most interesting aspects of your collection, making it unique?

13. Origin of the collection: Please indicate the proportion (%) of accessions on the total amount that were:
Collected originally in your own country (national origin)
Collected originally in your own region (regional origin)
Introduced from a collection abroad
From other origin (university, private collection)

14. Are there any major gaps in the collection?
Species coverage of the crop
Population (sample) representation per species
Ecological representation of the species
Other major gaps (please specify)

15. If there are major gaps, are there any plans to fill such gaps?
   Yes   No   Don't know If YES, briefly describe plans.

16. Please list the 5 major limitations you are facing in the management of the collection.

17. Please indicate the % proportion of accessions by type of germplasm
Wild related species
Landraces
Obsolete improved varieties
Advanced improved varieties
Breeding/research materials
Inter-specific derivatives Unknown
Other

18. Please describe the main potential/importance of your collection for use and breeding.

19. Has your Cucurbitaceae collection undergone morphological characterization?
   Yes   No   Don't know
If YES, to which extent? Please indicate proportion (%).

20. Has your Cucurbitaceae collection at least partially been screened for biotic stresses?
   Yes   No   Don't know
If YES, for which major diseases or insect pests?

21. Has your Cucurbitaceae collection at least partially been screened for abiotic stresses?
   Yes   No   Don't know
If YES, for which abiotic stresses?

Conservation status (germplasm management)

22. Please indicate the current and expected situations of the collection with respect to the following factors, where: 1 = high/good, 2 = adequate/moderate, 3 = not sufficient/bad, NA = not applicable:
   Current situation   Expected situation in the next 3 years
Funding for routine operations and maintenance
Retention of trained staff
Interest for Plant Genetic Resource Conservation by donors
Genetic variability in the collection as needed by users/breeders
Access to germplasm information (passport, characterization, evaluation)
Active support/feedback by users
Level of use by breeders

23. Storage form: Please indicate the % proportion of the accessions stored as:
Seeds
Field accessions
In vitro
Cryopreservation Pollen
DNA
Other

24. Conservation facilities: Please indicate the % proportion of the accessions maintained under the following conditions:
(Note: if accessions are maintained under more than one storage condition the total percentage may exceed 100%)
Short-term storage
Medium-term storage
Long-term storage
Other

25. Please describe the storage facilities: Storage facility (1)
Type of facility
Temperature
Relative Humidity (%)
Packing material
Other

26. Please describe the storage facilities: Storage facility (2)
Type of facility
Temperature
Relative Humidity (%)
Packing material
Other

27. Have you established a genebank management system or written procedures and protocols for:
YES   NO
Acquisition (including collecting, introduction and exchange)
Regeneration
Characterization
Storage and maintenance
Documentation
Health of germplasm
Distribution
Safety duplication
Other (please specify)

28. In case you have procedures and protocols, are you able to provide the Crop Trust with this information (i.e. provide a copy of the written procedures and protocols)?
   Yes   No   Don't know

29. Please describe your quality control activities (in terms of frequency and protocols/methods).
Germination tests
Viability testing
Health testing
True-to-typeness of in vitro plantlets
Other, please specify:

30. How many accessions require urgent regeneration (apart from the normal routine regeneration)?

Safety duplication

Safety duplication is defined as the storage of a duplicate/copy of an accession in another location for safety back-up in case of loss of the original accession.

31. Are accessions safety duplicated in another genebank?
   Yes   No   Don't know

32. Are there any constraints to duplicating the collection elsewhere outside your country?
   Yes   No   Don't know
If YES, please specify constraint.

33. To what extent do you consider the Cucurbitaceae accessions in your collection to be unique and not duplicated extensively elsewhere?
   Fully unique   Mostly unique   Partially unique   Fully duplicated elsewhere

If you safety duplicate in another genebank, please provide information below. Skip the following if not applicable and Go to Next page.

34. If accessions are safety duplicated in another genebank (1), please specify:
Name of institute maintaining your safety duplicates (1)
Number of accessions
Storage conditions (short, medium, long term)
Nature of the storage (e.g. black box, fully integrated in host collection, etc.)

35. If accessions are safety duplicated in another genebank (2), please specify:
Name of institute maintaining your safety duplicates (2)
Number of accessions
Storage conditions (short, medium, long term)
Nature of the storage (e.g. black box, fully integrated in host collection, etc.)

36. Is there any germplasm of other Cucurbitaceae collections safety duplicated at your facilities?
   Yes   No
If YES, please provide information on safety duplication at your genebank. Skip the following if not applicable and Go to Next page.

37. If accessions from other collections are safety duplicated at your genebank (1), please specify:
Name of holder of the original collection (1)
Number of accessions
Storage conditions (short, medium, long term)
Nature of the storage (e.g. black box, fully integrated in host collection, etc.)

38. If accessions from other collections are safety duplicated at your genebank (2), please specify:
Name of holder of the original collection (2)
Number of accessions
Storage conditions (short, medium, long term)
Nature of the storage (e.g. black box, fully integrated in host collection, etc.)

Information management

39. Do you use an electronic information system for managing the collection (data related to storage, germination, distribution, etc.)?
   Yes   No   Partly
If YES, what software is used? If NO, are there plans to do so in the future?

40. Is information of the collection accessible through the Internet?
   Yes   No   Partly

41. Do you have following types of data (passport, characterization, and evaluation) available in electronic format?
To a large extent   To some extent   No   Don't know
Passport data
Characterization data
Evaluation data

42. Are data of the collection included in other databases?
National
Regional
International
If yes or partly , specify the databases:

Distribution

43. Do you distribute accessions from your collection?
   Yes   No If NO, why not?

44. Do you use Material Transfer Agreement?
   Yes   No   Don't know

45. Do you set specific conditions for distribution? Please specify:

46. Do you keep records of the distribution?
   Yes   No   Don't know

47. What is the total number of accessions that are typically distributed annually (average of last 3 years)?
Within your country?
Outside your country?

48. How do you expect the number of accessions distributed to change for the next 3-5 years?
Within your country?
Outside your country?

49. What are the most important factors limiting the use of the material maintained in your collection?

50. Are germplasm materials sufficiently available in terms of QUANTITY and HEALTH for distribution?
Yes   No   Don't know
Seeds
In vitro material
Cryopreserved material
Other materials

51. Is the collection affected by diseases that can restrict the distribution of the germplasm?
   Yes, to large extent   Yes, to some extent   No   Don't know
If you answered Yes , are knowledge and facilities available at your institution for eradication of these diseases?

52. Which type of users received germplasm from you? Please estimate % proportion of total distribution in the past 3 years.
Farmers and farmers' organizations
Other genebank curators
Academic researchers and students
Plant breeders - public sector
Plant breeders - private sector
NGOs
Others

53. How do you inform potential users about the availability of accessions and their respective data in your collection?

54. Do you have adequate procedures in place for:
Phytosanitary certification
Packaging

55. Do you charge fees for the following?
Yes, for the cost of accessions Yes, for the cost of shipment
Yes, for both costs of accessions and shipment No
 If YES, briefly describe fee policy and indicate fee amount.

Collaboration

Collaboration with other genebanks and/or breeders of the public or private sector in terms of germplasm management

56. Does your genebank collaborate with other genebanks and/or breeders of the public and/or private sector on aspects of germplasm management (regeneration, characterization, preliminary evaluation), apart from safety duplication?
    Yes   No   Don't know

57. If YES, please provide information on your collaboration. Skip the following if not applicable and Go to Next page.
If YES, please provide the following information on your collaboration: (1)
A – Name of institution/ Location / Type (public or private)
B – Area of collaboration (regeneration, characterization, preliminary evaluation)

58. If YES, please provide the following information on your collaboration: (2)
A – Name of institution/ Location / Type (public or private)
B – Area of collaboration (regeneration, characterization, preliminary evaluation)

59. If YES, please provide the following information on your collaboration: (3)
A – Name of institution/ Location / Type (public or private)
B – Area of collaboration (regeneration, characterization, preliminary evaluation)

60. If YES, please provide the following information on your collaboration: (4)
A – Name of institution/ Location / Type (public or private)
B – Area of collaboration (regeneration, characterization, preliminary evaluation)

Collaboration

61. Do you collaborate in (a) network(s) as a Cucurbitaceae collection holder?
Yes   No   Don't know

If YES, please provide information on your networks. Skip the following if not applicable and Go to Next page.

62. If YES, please provide the following information for each of the networks: (1)
A – Name of network
B – Reasons for participation

63. If YES, please provide the following information for each of the networks: (2)
A – Name of network
B – Reasons for participation

Thank you very much!

If you have any questions about this questionnaire or about the proposed strategy in general, please contact maarten.vanzonneveld@worldveg.org and/or ebert.andreas6@gmail.com.

APPENDIX VII. SELECTED METRICS COLLECTED BY KHOURY ET AL. (2021) FOR CUCURBITS AND TOMATO

This appendix was written by Dr. Felix Frey, International Consultant, Global Crop Diversity Trust

Khoury et al. (2021) compiled a comprehensive dataset as part of a project funded by the International Treaty on Plant Genetic Resources for Food and Agriculture and the Crop Trust, led by the International Center for Tropical Agriculture (CIAT).

The aim was to introduce five normalized reproducible indicators to serve as an evidence base for use when prioritizing actions on the conservation and use of plant genetic resources for food and agriculture. The indicators encompass metrics associated with the USE of a crop (Global importance), the INTERDEPENDENCE between countries with respect to genetic resources, the DEMAND among researchers for genetic resources, the SUPPLY of germplasm by genebanks and the SECURITY of germplasm conservation. Graphs of the indicator results are publicly available on an interactive website. To generate the five indicators, Khoury et al. (2021) collected a comprehensive dataset from multiple sources. We do not present those indicators here, but rather discuss the underlying raw data to shed light on the aspects represented by the indicators.

Cucurbits represent a diverse family of crops. We present here the most important cucurbit crops which were examined by Khoury et al. (2021) (Table 1 & 3). By use they can be divided into fruits – watermelons (*Citrullus lanatus* & *C. vulgaris*) and melons (*Cucumis melo*) – and vegetables – cucumbers and gherkins (*Cucumis sativus*), West Indian gherkin (*Cucumis anguria*), zucchini (*Cucurbita pepo*), butternut squash (*Cucurbita moschata*), pumpkin (*Cucurbita maxima*), cushaw (*Cucurbita argyrosperma*), fig leaf gourd (*Cucurbita ficifolia*), calabash (*Lagenaria siceraria*), snake gourd (*Trichosanthes cucumerina*) and wax gourd (*Benincasa hispida* & *B. pruriens*) (Table 2). The mentioned cucurbits are taxonomically associated with the genera *Citrullus*, *Cucumis*, *Cucurbita*, *Trichosanthes* and *Benincasa*. To put some numbers into context, we compare cucurbits with tomatoes (Table 1). Both crop families / crops are comparable with respect to type of use (both are mostly used as vegetables) and the botanical fruit is the part which is consumed – cooked or raw. Tomatoes are represented here by the genus *Solanum* and by the single species *Solanum lycopersicum*. Results obtained for the genus *Solanum* are also attributed to other *Solanum* species, foremost potato (*Solanum tuberosum*), and can thus be hugely overestimated.

The metrics for "Global production", "Food supply" and "Quantity exported globally" under the indicator domain "Crop use" are annual average values drawn from FAOSTAT data for the years 2010-2014 (Khoury et al., 2021). The respective metrics are not always reported for all cucurbits as e.g. for tomatoes, where FAOSTAT reports separate metrics. With respect to production and trade of cucurbits, FAOSTAT reports values separately for watermelons, melons and cucumbers & gherkins. Zucchini, butternut squash, pumpkin, cushaw, fig leaf gourd and calabash are reported summarized as "Pumpkins, squash and gourds", i.e. numbers presented here represent the sum of production and trade (export) across the different species. Other cucurbit species (West Indian gherkin, snake gourd, wax gourd) are not reported by FAOSTAT. The percentage of countries producing and consuming (being supplied with) the crop is calculated as the number of countries, where the respective crop is within the top 95% of most important crops divided by the number of countries that report respective numbers (can be different between metrics and crops). With respect to food supply, FAOSTAT summarizes various crops into categories. Cucurbits fall into two groups, "fruits, other" (watermelons and melons) and "vegetables, others" (cucumbers & gherkins, zucchini, butternut squash, pumpkin, cushaw, fig leaf gourd and calabash). Again, numbers for West Indian gherkin, snake gourd, wax gourd are not reported. Although numbers are not reported directly for single crops, Khoury et al. (2021) inferred the food supply values from the combined metrics reported for the crop groups. They first calculated the weights of crops within the categories by global production, e.g. global annual production of "fruits, other" is 6,369,071,941 t, watermelon production is 2,024,179,503. The weight of watermelons within "fruits, other" is thus 0.32 from 1.00. To finally calculate food supply (for e.g. watermelons), they segregated the "fruit, other" value by the weight of the respective crop included in the category. The same was done for crops falling into the category "vegetables, other". The global production of all cucurbits is at about 228 million tons annually, which is 1.4 times more than the global tomato production (160 M t). The biggest share with 47 % of cucurbit production falls on watermelons, with 104 M tons, followed by cucumbers and gherkins (69 M tons), melons (32 M tons) and "Pumpkins, squash and gourds", with a combined production of 24 M tons. Cucurbit production is widely distributed through the world, the indi-

vidual crops are produced in 49 – 63 % of countries worldwide, led by cucumbers, which are within the 95 % of most important crops in 63 % of countries with respect to production. In contrast to tomatoes, export importance is relatively low in cucurbits. Where 8 % of global tomato production is exported, only 4 % of cucurbits are exported. With respect to export, melons lead the cucurbits, with a 7 % export share of production, all the other cucurbits are 97 % used nationally (3 % export). The quantity of food supply by cucurbits, i.e. the average global consumption, ranges from 1.17 g/cap/day for "Pumpkins, squash and gourds" to 6.15 g/cap/day for watermelons. Food supply of all cucurbits combined is at 12.6 g/cap/day, compared to 55.5 g/cap/day for tomato. These numbers appear counterintuitive, we would suppose a higher food supply of cucurbits than that of tomatoes, given the fact that cucurbits global production is greater than that of tomatoes. The reason for this relationship could be related to the fact that cucurbits are reported in different summarized categories by FAOSTAT (e.g. "fruits, other" and "vegetables, other"), in contrast to tomatoes, which are reported directly and thus probably more reliable. Furthermore, a bigger share of cucurbits is not consumed (non-edible parts of fruits) and could thus be responsible for lower food supply values.

The crop use metrics with respect to research were assessed by manual search on google scholar, searching for the respective genus or species in the titles of publications, including patents and citations, between the years 2009 and 2019 (Khoury et al., 2021). Google scholar search hits represent importance with respect to scientific interest in a crop. As mentioned previously, the crop group of cucurbits includes the genera *Citrullus*, *Cucumis*, *Cucurbita*, *Trichosanthes* and *Benincasa*. All five genera yielded a total of 13,827 Google Scholar hits, which is lower than hits for tomato with 16,500. The genus *Cucumis* including melons and cucumbers is the most represented genus in the cucurbit group (6,040 hits). However, the tomato genus hits are highly overestimated as *Solanum* includes many more species, foremost the major crop of potato. More meaningful is, in this respect the google scholar hits for the respective species, with a total of 10,915 hits summarized across all cucurbits, where *Solanum lycopersicum* was only found 4,740 times on google scholar. Research interest within cucurbits was highest in cucumbers (2,970 hits) and melons (2,330 hits), whereas the cucurbit with the highest production, watermelon, was only found 1,330 times. Calabash and pumpkin (*Cucurbita maxima*) were mentioned on an intermediate level (701 and 537 hits, respectively). Research interest was relatively low in wax gourd (277), snake gourd (124), fig leaf gourd (84) and cushaw (69).

Khoury et al. (2021) defined interdependence as a measure for the degree of dependence of the global cultivation and use of a certain crop from germplasm present at the primary centers of diversity of the respective crop. Primary centers of diversity are not represented by countries, but by 23 agroecological zones (Khoury et al. 2016), as crop diversity does not follow national boarders but rather climatic and agroecological boundaries. Interdependence is high in crops which originate from a small area and are cultivated and used globally. For production, interdependence is calculated by dividing a crops' production outside of the primary centers of diversity by the global production. If all production would be outside the primary center of diversity, interdependence would be 100 %. For food supply, interdependence is calculated by dividing the food supply by the world average. Food supply outside can be higher than inside of primary regions of diversity and thus also higher than the global mean. Therefore, interdependence with respect to food supply can be above 100 %. Interdependence varies greatly within the cucurbit group mainly because the different crops originate from very different primary centers of diversity. Watermelons originate from West Africa, where they are today not predominantly grown, which leads to an interdependence of 100 % with respect to production, similar to the 98 % of tomato, which originates from Central and Andean America. The same is true for the crops in the group of "Pumpkins, squash and gourds", which have interdependence values between 94 and 99 %, calabash, for example, is cultivated all over the tropical regions of the world, has its center of origin in South Africa. These values should be taken with caution, as there are no reported production numbers for separate crops in this group, consequently interdependence cannot be assessed reliably. Melons and cucumbers have, with 25 and 18 % very low interdependence with respect to production. They originate both from a wide range of regions, where most of production is taking place today (melons originate from throughout Africa and Asia, cucumbers from East, South and South-East Asia). The average interdependence with respect to food supply (95 %) is higher in all cucurbit crops compared to average interdependence with respect to production (81 %). It is especially high in melons, where food supply interdependence is 92 %, production interdependence is 25 %. This is putatively because a huge share of produced melons is exported (7 %), as mentioned previously, to countries outside of the centers of diversity. This may however be an artefact due to inclusion of both, watermelon and melon in one category with respect to food supply ("fruits, other").

Demand for germplasm is defined by two metrics (Khoury et al., 2021). First, by the number of distri-

butions of accessions by gene banks, as an annual average between 2014 and 2017 drawn from the Plant Treaty Information System. Second, by the number of varieties released during the five years between 2014 and 2018, obtained from the International Union for the Protection of New Varieties of Plants (UPOV). A high number of accessions of cucurbits were distributed by gene banks annually (33,086 accessions), which is three times more than distributions of tomato accessions. However, this number seems to be inflated by counting distributions multiple times within the group of crops in the genus *Cucurbita*, where the data shows around 3,000 distributions per crop. The distribution numbers for the five crops (zucchini, butternut squash, pumpkin, cushaw and fig leaf gourd) are very similar for the different crops, where one would expect highly diverging numbers, and much lower number for cushaw and fig leaf gourd with much lower importance compared to e.g. zucchini. The numbers could be inflated by the number distributions of accessions which were attributed to the genus *Cucurbita*. Within five years 27,740 varieties of different cucurbits have been released, the highest share was cucumbers with 11,896 cultivars, followed by melons (7,198), watermelons (3,684) and zucchini (3,778). The number of released cucurbit varieties was similar to the number of tomato varieties released within five years (30,367).

Khoury et al. (2021) illustrated the supply of germplasm with the number of accessions available in *ex situ* collections around the world, with respect to the crop genus and the most important species of the respective crop. Furthermore, Khoury et al. (2021) assessed the number of accessions (again with respect to genus and species) available under the multilateral system (MLS) of the Plant Treaty. This was done first, directly, as notation (in MLS / not in MLS) in the public online databases Genesys, FAO WIEWS and GBIF.

Secondly, the availability of accessions was assessed by considering whether the country hosting the institution that held the respective germplasm collection was a signatory to the Plant Treaty, in which case, the accession was regarded as available via the MLS. Cucurbits are well represented in international germplasm collections with a total of 76,970 and 66,850 accessions, regarding the genus and species level. This is twice of the amount of accessions held in global tomato collections (39,305). Most of cucurbit accessions are attributed to melons (13,234), cucumbers (11,766) and watermelons (10,337). None of the cucurbit crops (nor tomato) are listed in Annex I of the Plant Treaty, consequently accessions could not be stated to be available under MLS with reference to the holding institutions' country. Nevertheless, on average 10 % of cucurbit accessions were assigned to be avail-

able under the MLS, stated directly in the databases. The percentage of accessions available under MLS highly differs between the different cucurbit crops, ranging from 1% (watermelon) to 31% (Snake gourd).

Security of germplasm conservation is represented here with two metrics, the safety duplication status at the Svalbard Global Seed Vault (SGSV) and the equality of global distribution with respect to several crop use metrics. The numbers of accessions safety duplicated with respect to genus and species were taken from the website of the SGSV and divided by the total number of accessions stored in global ex situ collections (see paragraph above), with the result giving the percentage of safety duplicated germplasm. To represent the equality of distribution across different agroecological regions of the world (Khoury et al., 2016), Khoury et al. (2021) used the reciprocal 1-Gini index with respect to the different crop use metrics. The Gini index is the most commonly used inequality index (Gini index, 2008), known foremost for the quantification of global income inequality. The 1-Gini index, presented here, ranges from 0 to 1, where 0 reflects very unequal distribution across world regions and 1 reflects a completely equal global distribution across regions. It reflects the security of crop cultivation and use, where, for example, small indices of production and thus geographic restriction go hand in hand with a higher vulnerability of supply, as in the case of natural disasters. A moderate proportion of cucurbit accessions held in global germplasm collections are safety duplicated at SGSV. On the level of the different cucurbit genera, on average 5% (0 – 11 %) of accessions are duplicated at SGSV, where on average 27% (1–92%) are duplicated if we regard the single species of cucurbits. Within the economically three most important cucurbit crops (production-wise), cucumber and melon accessions are duplicated with a relatively high rate of 24 and 21%, whereas only 4% of copies of watermelon accessions are present at SGSV. There is thus a strong need to intensify efforts for replication of watermelon germplasm to ensure safe long-term conservation. This is especially important if we compare safety duplication of most cucurbit crops with the rate of safety duplication of tomato accessions, which is, with 80 %, relatively high. Equality of the distribution across agroecological zones with respect to production of cucurbits is on average relatively low (0.02), compared to tomatoes (0.04). The small value of equality of distribution of cucurbits is attributed to the most important cucurbit crops watermelon, melon and cucumber with values around 0.02. On the contrary, the equality of distribution of the production of the "Pumpkin, squash and gourds" group is, with 0.04, equally high as for tomatoes. Equality of distribution of food supply with cucurbits (0.26 on average) is higher than the one for

tomatoes. However, as mentioned previously food supply numbers have to be treated with caution, as several cucurbit crops are reported summarized by FAOSTAT.

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Table 1. Selected metrics collected by Khoury et al. 2021 for cucurbit crops and tomato, subdivided by indicator domain.

Metric	Cucurbits (sum/range)	Tomatoes	Cucurbits / Tomatoes
Crop use			
Global production [tons] (Sum across cucurbit species)	228,059,816	160,252,190	142%
Percentage of countries producing crop (Range) *	49-63%	81%	77%
Quantity exported globally [t] (Sum across cucurbit species)	8,245,983	12,048,216	68%
Food supply (Amount consumed) [g/capita/day] (Sum across cucurbit species)	13	55	23%
Number of publications between 2009-2019, including patents and citations, searching title of publication (Google scholar search hits) for genus (Sum across cucurbit species) **	13,827	16,500	84%
Number of publications between 2009-2019, including patents and citations, searching title of publication (Google scholar search hits) for species (Sum across cucurbit species) ***	10,915	4,740	230%
Interdependence			
Interdependence of global production from germplasm from primary centers of diversity [0-1] (Range) ****	25-100%	98%	
Interdependence of global food supply from germplasm from primary centers of diversity [0-1] (Range) ****	44-107%	102%	
Demand			
Accessions distributed from gene banks (Annual average 2014-2017) (Sum across cucurbit species)	33,086	10,967	302%
Variety releases in 5 years (2014-2018) (Sum across cucurbit species)	27,740	30,367	91%
Supply			
Number of accessions in *ex situ* collections of genus (Sum across cucurbit species) **	76,970	122,252	63%
Number of accessions in *ex situ* collections of species (Sum across cucurbit species) ***	66,850	39,305	170%
Accessions of the genus ** available through Multilateral System (MLS) directly noted in databases (Range) [%]	1-29%	32%	
Accessions of the species *** available through Multilateral System (MLS) directly noted in databases (Range) [%]	1-31%	22%	
Accessions of the genus ** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%	
Accessions of the species *** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%	
Security			
Accessions of genus ** safety duplicated in Svalbard Global Seed Vault (Range) [%]	0-11%	14%	
Accessions of species *** safety duplicated in Svalbard Global Seed Vault (Range) [%]	1-92%	34%	
1-GINI index for equality of production across the world [0-1] (Range) *****	0.2-0.4	0.04	
1-GINI index for equality of food supply across the world [0-1] (Range) *****	0.25-0.27	0.19	

* Counting countries which list the crop as within top 95% (FAOSTAT); Calculated as: Number of countries counting crop (top 95%) / Total number of countries (production 216, food supply 175)
** Cucurbits: Genus names, Table 2; Tomato: *Solanum*
*** Cucurbits: Speices names, Table 2; Tomato: *Solanum tuberosum*
**** Global metric / Metric at primary center of diversity
***** Relative equality of crop use across world regions (same regions as used in interdependence domain), high equality give high indicator value

Table 2. Cucurbit crops, corresponding genus, species, FAO stat category and origin.

Crop	Genus	Species	FAO stat category	Origin
Watermelons	*Citrullus*	*Citrullus lanatus, Citrullus vulgaris*	Watermelons (production/trade) / Fruits, other (food supply)	West Africa
Melons	*Cucumis*	*Cucumis melo*	Melons (production/trade) / Fruits, other (food supply)	South, East and West Africa, West, South, East and South-East Asia
Cucumbers and gherkins	*Cucumis*	*Cucumis sativus*	Cucumbers and gherkins (production/trade) / Vegetables, other (food supply)	South, East and South-East Asia
West Indian Gherkin	*Cucumis*	*Cucumis anguria*	Not reported by FAOSTAT	Central, East and South Africa
Zucchini	*Cucurbita*	*Cucurbita pepo*	Pumpkins, squash and gourds (production/trade) / Vegetables, Other (food supply)	Central America
Butternut squash	*Cucurbita*	*Cucurbita moschata*	Pumpkins, squash and gourds (production/trade) / Vegetables, Other (food supply)	North, Central and tropical South America
Pumpkin	*Cucurbita*	*Cucurbita maxima*	Pumpkins, squash and gourds (production/trade) / Vegetables, Other (food supply)	Tropical South America
Cushaw	*Cucurbita*	*Cucurbita argyrosperma*	Pumpkins, squash and gourds (production/trade) / Vegetables, Other (food supply)	Central America
Fig leaf gourd	*Cucurbita*	*Cucurbita ficifolia*	Pumpkins, squash and gourds (production/trade) / Vegetables, Other (food supply)	Central, andean and tropical South America
Calabash	*Lagenaria*	*Lagenaria siceraria*	Pumpkins, squash and gourds (production/trade) / Vegetables, Other (food supply)	South Africa
Snake gourd	*Trichosanthes*	*Trichosanthes cucumerina*	Not reported by FAOSTAT	South, East and South-East Asia
Wax gourd	*Benincasa*	*Benincasa hispida, B. pruriens*	Not reported by FAOSTAT	South and South-East Asia

Table 3. Table of indicator values for species within cucurbit crops.

Metric	Watermelons	Melons	Cucumbers and gherkins	West Indian Gherkin
Crop use				
-- Category within FAOSTAT production / trade	**Watermelons**	**Melons**	**Cucumbers and gherkins**	**Not in FAOSTAT**
Global production [tons] (Sum across cucurbit species)	104,237,097	31,586,955	68,519,552	NA
Percentage of countries producing crop (Range) *	55%	49%	63%	NA
Quantity exported globally [t] (Sum across cucurbit species)	2,928,486	2,151,903	2,377,359	NA
-- Category within FAOSTAT food supply	**Fruits, Other**		**Vegetables, Other**	**Not in FAOSTAT**
Food supply (Amount consumed) [g/capita/day] (Sum across cucurbit species)	6.15	1.85	3.40	NA
Number of publications between 2009-2019, including patents and citations, searching title of publication (Google scholar search hits) for genus (Sum across cucurbit species) **	2,440	6,040		
Number of publications between 2009-2019, including patents and citations, searching title of publication (Google scholar search hits) for species (Sum across cucurbit species) ***	1,330	2,330	2,970	83
Interdependence				
Interdependence of global production from germplasm from primary centers of diversity [0-1] (Range) ****	100%	25%	18%	NA
Interdependence of global food supply from germplasm from primary centers of diversity [0-1] (Range) ****	102%	92%	44%	NA
Demand				
Accessions distributed from gene banks (Annual average 2014–2017) (Sum across cucurbit species)	2,731	4,857	5,025	4,807
Variety releases in 5 years (2014–2018) (Sum across cucurbit species)	3,684	7,198	11,896	15
Supply				
Number of accessions in *ex situ* collections of genus (Sum across cucurbit species) **	11,082	29,007		
Number of accessions in *ex situ* collections of species (Sum across cucurbit species) ***	10,337	13,234	11,766	328
Accessions of the genus ** available through Multilateral System (MLS) directly noted in databases (Range) [%]	1%	6%		
Accessions of the species *** available through Multilateral System (MLS) directly noted in databases (Range) [%]	1%	2%	11%	6%
Accessions of the genus ** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%		
Accessions of the species *** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%	0%	0%
Security				
Accessions of genus ** safety duplicated in Svalbard Global Seed Vault (Range) [%]	4%	11%		
Accessions of species *** safety duplicated in Svalbard Global Seed Vault (Range) [%]	4%	21%	24%	92%
1-GINI index for equality of production across the world [0-1] (Range) *****	0.02	0.02	0.02	NA
1-GINI index for equality of food supply across the world [0-1] (Range) *****	0.27	0.27	0.25	NA

* Counting countries which list the crop as within top 95% (FAOSTAT); Calculated as: Number of countries counting crop (top 95%) / Total number of countries (production 216, food supply 175)
** Cucurbits: Genus names, Table 2; Tomato: *Solanum*
*** Cucurbits: Species names, Table 2; Tomato: *Solanum tuberosum*
**** Global metric / Metric at primary center of diversity
***** Relative equality of crop use across world regions (same regions as used in interdependence domain), high equality give high indicator value

Table 3. continuation

Metric	Zucchini	Butternut squash	Pumpkin	Cushaw	Fig leaf gourd	Calabash
Crop use						
-- Category within FAOSTAT production/trade	Pumpkins, squash and gourds (production is sum across this category)					
Global production [tons] (Sum across cucurbit species)	23,716,212					
Percentage of countries producing crop (Range) *	54%					
Quantity exported globally [t] (Sum across cucurbit species)	788,236					
-- Category within FAOSTAT food supply	Vegetables, Other					
Food supply (Amount consumed) [g/capita/day] (Sum across cucurbit species)	1.17					
Number of publications between 2009–2019, including patents and citations, searching title of publication (Google scholar search hits) for genus (Sum across cucurbit species) **	3,510 (zucchini, butternut squash, pumpkin, cushaw, fig leaf gourd)					82 (calabash)
Number of publications between 2009–2019, including patents and citations, searching title of publication (Google scholar search hits) for species (Sum across cucurbit species) ***	1,380	1,030	537	69	84	701
Interdependence						
Interdependence of global production from germplasm from primary centers of diversity [0-1] (Range) ****	98%	94%	99%	98%	96%	99%
Interdependence of global food supply from germplasm from primary centers of diversity [0-1] (Range) ****	101%	107%	103%	101%	106%	102%
Demand						
Accessions distributed from gene banks (Annual average 2014–2017) (Sum across cucurbit species)	3,164	3,019	3,021	3,019	3,019	379
Variety releases in 5 years (2014–2018) (Sum across cucurbit species)	3,778	209	872	1	12	71
Supply						
Number of accessions in *ex situ* collections of genus (Sum across cucurbit species) **	29,769 (zucchini, butternut squash, pumpkin, cushaw, fig leaf gourd)					4,926 (calabash)
Number of accessions in *ex situ* collections of species (Sum across cucurbit species) ***	8,076	9,662	6,486	921	664	4,114
Accessions of the genus ** available through Multilateral System (MLS) directly noted in databases (Range) [%]	7%					
Accessions of the species *** available through Multilateral System (MLS) directly noted in databases (Range) [%]	7%	9%	4%	8%	3%	8%
Accessions of the genus ** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%					
Accessions of the species *** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%	0%	0%	0%	0%
Security						
Accessions of genus ** safety duplicated in Svalbard Global Seed Vault (Range) [%]	5%					
Accessions of species *** safety duplicated in Svalbard Global Seed Vault (Range) [%]	16%	13%	19%	62%	69%	4%
1-GINI index for equality of production across the world [0-1] (Range) *****	0.04					
1-GINI index for equality of food supply across the world [0-1] (Range) *****	0.26					

Table 3. continuation

Metric	Snake gourd	Wax gourd
Crop use		
-- Category within FAOSTAT production / trade	**Not in FAOSTAT**	
Global production [tons] (Sum across cucurbit species)	NA	NA
Percentage of countries producing crop (Range) *	NA	NA
Quantity exported globally [t] (Sum across cucurbit species)	NA	NA
-- Category within FAOSTAT food supply	**Not in FAOSTAT**	
Food supply (Amount consumed) [g/capita/day] (Sum across cucurbit species)	NA	NA
Number of publications between 2009-2019, including patents and citations, searching title of publication (Google scholar search hits) for genus (Sum across cucurbit species) **	647	365
Number of publications between 2009-2019, including patents and citations, searching title of publication (Google scholar search hits) for species (Sum across cucurbit species) ***	124	277
Interdependence		
Interdependence of global production from germplasm from primary centers of diversity [0-1] (Range) ****	NA	NA
Interdependence of global food supply from germplasm from primary centers of diversity [0-1] (Range) ****	NA	NA
Demand		
Accessions distributed from gene banks (Annual average 2014-2017) (Sum across cucurbit species)	NA	47
Variety releases in 5 years (2014-2018) (Sum across cucurbit species)	0	4
Supply		
Number of accessions in *ex situ* collections of genus (Sum across cucurbit species) **	1,079	1,107
Number of accessions in *ex situ* collections of species (Sum across cucurbit species) ***	230	1,032
Accessions of the genus ** available through Multilateral System (MLS) directly noted in databases (Range) [%]	7%	29%
Accessions of the species *** available through Multilateral System (MLS) directly noted in databases (Range) [%]	31%	28%
Accessions of the genus ** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%
Accessions of the species *** available through Multilateral System (MLS) indirectly by matching institute countries with party status [%]	0%	0%
Security		
Accessions of genus ** safety duplicated in Svalbard Global Seed Vault (Range) [%]	0%	3%
Accessions of species *** safety duplicated in Svalbard Global Seed Vault (Range) [%]	1%	3%
1-GINI index for equality of production across the world [0-1] (Range) *****	NA	NA
1-GINI index for equality of food supply across the world [0-1] (Range) *****	NA	NA

* Counting countries which list the crop as within top 95% (FAOSTAT); Calculated as: Number of countries counting crop (top 95%) / Total number of countries (production 216, food supply 175)
** Cucurbits: Genus names, Table 2; Tomato: *Solanum*
*** Cucurbits: Species names, Table 2; Tomato: *Solanum tuberosum*
**** Global metric / Metric at primary center of diversity
***** Relative equality of crop use across world regions (same regions as used in interdependence domain), high equality give high indicator value

APPENDIX VIII. GENETIC DIVERSITY OF CUCURBITACEAE FOUND IN INDIA

Table 1. Areas of India containing a rich diversity of landraces and primitive cultivars for various Cucurbitaceae crops (adapted from: Chithra Devi Pandey, ICAR-NBPGR, India).

Crop Scientific Name	Crop Common Name	Diversity Rich Areas
Benincasa hispida	Wax gourd	Bihar, Assam, Uttar Pradesh, Orissa, West Bengal
Coccinia grandis	Ivy gourd	Eastern and southern Uttar Pradesh, eastern Bihar, Chhattisgarh (tribal tract), West Bengal, North-eastern hill region
Cucumis anguria	West Indian gherkins	Tamil Nadu (drier tracts)
Cucumis melo	Muskmelon	Indo-Gangetic plains (landraces), Uttar Pradesh, Rajasthan, Karnataka, Andhra Pradesh, Haryana, Punjab, Mizoram, Karnataka
Cucumis sativus	Cucumber	Himalaya (local types/ landraces), southern Maharashtra
Cucumis sativus var. *sikkimensis*	Sikkim cucumber	Uttarakhand (Pithoragarh, Naintal) and areas adjoining Bhutan and Nepal; North Eastern Hill region (Manipur, Nagaland, Meghalaya)
Cucurbita spp.	Pumpkins and squash	North Eastern Hill region, Western Ghats, Andaman and Nicobar Islands
Cyclanthera pedata	Meetha karela, achocha, or stuffing cucumber	Meghalaya, Manipur, Nagaland, Andhra Pradesh, Arunachal Pradesh
Lagenaria siceraria	Bottle gourd	Orisha, Chhattisgarh (mainly tribal tracts)
Luffa acutangula and *Luffa cylindrica*	Angled and smooth loofah	Indo-Gangetic plains (landraces), Terai region, north-eastern plains (hermaphrodite forms), Tripura, Nagaland (aromatic leaf edible)
Momordica charantia	Bitter gourd	Terai region (Uttarakhand), Bihar, Maharashtra and North-Eastern region (landraces/local types)
Momordica cochinchinensis	Gac	Tribal parts of Bihar, Jharkhand, Orissa, Maharashtra, Assam
Momordica dioica	Spiny gourd	Madhya Pradesh, Tamil Nadu, Bihar, Jharkhand, West Bengal, Odisha
Praecitrullus fistulosus	Indian round gourd	Western Uttar Pradesh, Haryana, Punjab (landraces)
Trichosanthes cucumerina	Snake gourd	Southern peninsular tract, Kerala, eastern & western peninsular, north-eastern region (landraces)
Trichosanthes dioica	Pointed gourd	Gorakhpur (Eastern Uttar Pradesh), Bihar and adjoining Bengal plains (landraces); Assam plains and Tripura valley (semi-domesticated types)

Table 2. Wild relatives of Cucurbitaceae crops in different regions of India (adapted from: Chithra Devi Pandey, ICAR-NBPGR, India).

Region	Crop Wild Relatives
Western Himalayas	*Cucumis sativus* var. *hardwickii, Cucumis melo, Luffa echinata, Luffa graveolens, Trichosanthes multiloba, Trichosanthes pilosa*
Eastern Himalayas	*Cucumis melo, Luffa graveolens*
North-eastern hills	*Cucumis hystrix, Cucumis melo, Luffa graveolens, Momordica cochinchinensis, Momordica dioica, Momordica subangulata, Trichosanthes cucumerina, Trichosanthes dioica, Trichosanthes khasiana* (unresolved name), *Trichosanthes truncata* (unresolved name)
Gangetic plains	*Luffa echinata, Momordica cochinchinensis, Momordica cymbalaria, Momordica dioica*
Indus plains	*Citrullus colocynthis, Cucumis prophetarum, Momordica balsamina*
Western peninsular tracts	*Cucumis melo, Cucumis setosus, Luffa graveolens, Momordica cochinchinensis, Momordica subangulata, Trichosanthes anaimalaiensis* (unresolved name), *Trichosanthes cuspidata* (unresolved name), *Trichosanthes nervifolia* (unresolved name), *Trichosanthes tricuspidata, Trichosanthes villosa*
Eastern peninsular tracts	*Cucumis hystrix, Cucumis setosus, Luffa acutangula, Luffa graveolens, Luffa umbellata* (unresolved name), *Momordica cymbalaria, Momordica denticulata* (unresolved name), *Momordica dioica, Momordica subangulata, Trichosanthes cordata, Trichosanthes lepiniana, Trichosanthes multiloba, Trichosanthes pilosa, Trichosanthes tricuspidata*
Islands	*Momordica* spp. *and Trichosanthes* spp.

APPENDIX IX. CUCUMIS TAXA AND CORRESPONDING NUMBER OF ACCESSIONS CONSERVED GLOBALLY

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020).

Taxon	Accessions[1]	Biological Status
Cucumis melo L.	10,682	Cultivated
Cucumis melo subsp. *agrestis* (Naudin) Pangalo	169	Cultivated
Cucumis melo subsp. *melo* L.	3,172	Cultivated
Cucumis melo subsp. *orientale* Sageret ex Filov	1	Cultivated
Cucumis melo var. *agrestis* Naudin	65	Wild
Cucumis melo L. group Cantalupensis	170	Cultivated
Cucumis melo L. group Chito	3	Feral
Cucumis melo L. group *Conomon*	391	Cultivated
Cucumis melo var. *cultus* Kurz	1	Cultivated
Cucumis melo L. group Flexuosus	241	Cultivated
Cucumis melo L. group Inodorus	27	Cultivated
Cucumis melo L. group Momordica	202	Cultivated
Cucumis melo var. *texanus* Naudin	45	Wild
Cucumis melo L. group Makuwa	426	Cultivated
Cucumis melo L. group Ibericus	22	Cultivated
Cucumis melo L. group Ameri	2	Cultivated
Cucumis melo L. group Dudaim	2	Cultivated
Cucumis melo L. group Cassaba	1	Cultivated
Cucumis melo L. group Kachri	1	Cultivated
Cucumis sativus L.	9,345	Cultivated
Cucumis sativus var. *hardwickii* (Royle) Alef.	174	Wild
Cucumis sativus var. *sativus*	2,012	Cultivated
Cucumis sativus var. *sikkimensis* Hook. f.	5	Cultivated
Cucumis sativus var. *xishuangbannanesis ined.*	1	Cultivated
Cucumis anguria L.	314	Cultivated
Cucumis anguria var. *anguria*	13	Wild
Cucumis anguria var. *longaculeatus* J. H. Kirkbr.	23	Wild
Cucumis metuliferus E. Mey. ex Naudin	157	Cultivated
Cucumis zambianus Widrlechner et al.	15	Cultivated
Cucumis esculentus Salisb.	1	Cultivated
Cucumis setosus Cogn.	1	Cultivated
Cucumis silentvalleyi (Manilal et al.) Ghebret. & Thulin	1	Cultivated
Cucumis callosus Cogn. (Synonym of *C. trigonus Roxb.*)	197	Wild
Cucumis africanus L. f.	98	Wild
Cucumis dipsaceus Ehrenb. ex Spach	94	Wild
Cucumis prophetarum L.	79	Wild

Taxon	Accessions[1]	Biological Status
Cucumis myriocarpus Naudin	58	Wild
Cucumis zeyheri Sond.	46	Wild
Cucumis pustulatus Hook. f.	31	Wild
Cucumis ficifolius A. Rich.	25	Wild
Cucumis trigonus Roxb.	18	Wild
Cucumis sagittatus Peyr.	17	Wild
Cucumis maderaspatanus L.	15	Wild
Cucumis myriocarpus subsp. *myriocarpus* Naudin	12	Wild
Cucumis aculeatus Cogn.	9	Wild
Cucumis hystrix Chakrav.	9	Wild
Cucumis meeusei C. Jeffrey	9	Wild
Cucumis heptadactylus Naudin	8	Wild
Cucumis myriocarpus subsp. *leptodermis* (Schweick.) C. Jeffrey & P. Halliday	6	Wild
Cucumis hirsutus Sond.	5	Wild
Cucumis javanicus (Miq.) Ghebret. & Thulin	3	Wild
Cucumis kalahariensis A. Meeuse	3	Wild
Cucumis prophetarum subsp. *prophetarum* L.	3	Wild
Cucumis leiospermus (Wight & Arn.) Ghebret. & Thulin	2	Wild
Cucumis sacleuxii Pailleux & Bois	2	Wild
Cucumis argenteus (Domin) P. Sebastian & I. Telford	1	Wild
Cucumis asper Cogn.	1	Wild
Cucumis globosus C. Jeffrey	1	Wild
Cucumis humifructus Stent	1	Wild
Cucumis muriculatus Chakrav.	1	Wild
Cucumis prophetarum subsp. *dissectus* (Naudin) C. Jeffrey	1	Wild
Cucumis quintanilhae R. Fern. & A. Fern.	1	Wild
Cucumis subsericeus Hook. f.	1	Wild
Cucumis vulgaris E.H.L.Krause	1	Wild
Cucumis sp.	854	Wild and Cultivated
Total	**29,297**	**Wild and Cultivated**

[1]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

APPENDIX X. MAJOR HOLDING INSTITUTES OF *CUCUMIS* ACCESSIONS

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020) and strategy survey responses.

Holding Institute	Databases	Survey	Survey and Databases	% of Total	Country or Area
RUS001		6,829	6,829	17.378	Russian Federation
USA020	4,951		4,943	12.579	United States of America
JPN183	4,684		4,684	11.920	Japan
IND001	2,009		1,931	4.914	India
CHN001		1,500	1,500	3.817	China
DEU146	1,171	1,170	1,170	2.977	Germany
ESP027	1,110		1,110	2.825	Spain
BGR001	1,032		1,032	2.626	Bulgaria
NLD037	1,005	1,067	1,067	2.715	Netherlands
ESP026	953	1,318	1,318	3.354	Spain
CZE122	932	938	938	2.387	Czechia
BGD206	899		899	2.288	Bangladesh
POL003	767	767	767	1.952	Poland
UZB006		676	676	1.720	Uzbekistan
USA974	732		732	1.863	United States of America
TWN001	643	644	644	1.639	International
MAR088	621		621	1.580	Morocco
ESP058	540		540	1.374	Spain
HUN003	533		533	1.356	Hungary
SDN002	486		486	1.237	Sudan
UKR021	455		455	1.158	Ukraine
USA005	452		452	1.150	United States of America
MNG030	432		432	1.099	Mongolia
BRA017	370	224	224	0.570	Brazil
BGD003	366		366	0.931	Bangladesh
BRA003	356		356	0.906	Brazil
PRT001	275	275	275	0.700	Portugal
ZMB048	261		261	0.664	Zambia
UKR048	234		234	0.595	Ukraine
FRA011	200		200	0.509	France
ARM059	188		188	0.478	Armenia
ROM007	164	192	192	0.489	Romania
KEN212	162		162	0.412	Kenya
ITA392	140		140	0.356	Italy
PAK001	138		138	0.351	Pakistan
SWE054	135	106	106	0.270	Sweden
TZA016	122		122	0.310	United Republic of Tanzania
CAN004	118		118	0.300	Canada

[2]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

Holding Institute	Databases	Survey	Survey and Databases	% of Total	Country or Area
JOR015	97		97	0.247	Jordan
JOR105	97		97	0.247	Jordan
ARG013		94	94	0.239	Argentina
AZE015	94		94	0.239	Azerbaijan
ALB026	75		75	0.191	Albania
GBR004	74		74	0.188	United Kingdom of Great Britain and Northern Ireland
UKR025	71		71	0.181	Ukraine
BRA012	60	727	727	1.850	Brazil
TUR001	60		60	0.153	Turkey
LBY006	59		59	0.150	Libya
BRA020	56		56	0.143	Brazil
TUN029	54		54	0.137	Tunisia
ZAF062	50		50	0.127	South Africa
AUT046	42		42	0.107	Austria
ARE003	40		40	0.102	United Arab Emirates
ESP200	39		39	0.099	Spain
LKA036	38		38	0.097	Sri Lanka
ESP003	34		34	0.087	Spain
UKR008	33		33	0.084	Ukraine
USA158	31		31	0.079	United States of America
ESP133	30		30	0.076	Spain
CRI001	25	25	25	0.064	Costa Rica
SWZ015	24		24	0.061	Eswatini
GBR006	23		23	0.059	United Kingdom of Great Britain and Northern Ireland
AZE005	21		21	0.053	Azerbaijan
BOL317	21		21	0.053	Bolivia (Plurinational State of)
ARM005	20		20	0.051	Armenia
BWA015	20		20	0.051	Botswana
ESP198	19		19	0.048	Spain
LBN002	18		18	0.046	Lebanon
GBR017	16		16	0.041	United Kingdom of Great Britain and Northern Ireland
ITA393	16		16	0.041	Italy
MKD001	15		15	0.038	North Macedonia
BGD215	14		14	0.036	Bangladesh
ERI003	13		13	0.033	Eritrea
LTU006	13		13	0.033	Lithuania
AZE014	12		12	0.031	Azerbaijan
PRT025	12		12	0.031	Portugal
ISR002	11		11	0.028	Israel
BLR011	10		10	0.025	Belarus
CUB014	10		10	0.025	Cuba
ECU023	10		10	0.025	Ecuador
GRC005	10		10	0.025	Greece
LVA009	10		10	0.025	Latvia

Holding Institute	Databases	Survey	Survey and Databases	% of Total	Country or Area
ROM021	10		10	0.025	Romania
ROM019	9		9	0.023	Romania
THA300	9		9	0.023	Thailand
ARM035	8		8	0.020	Armenia
ITA363	8		8	0.020	Italy
LTU001	8		8	0.020	Lithuania
TTO010	7		7	0.018	Trinidad and Tobago
AUT047	6		6	0.015	Austria
CYP004	6		6	0.015	Cyprus
NAM006	6		6	0.015	Namibia
PRT102	6		6	0.015	Portugal
ZMB030	6		6	0.015	Zambia
ARG1342	5		5	0.013	Argentina
ARM008	5		5	0.013	Armenia
CHE001	5	36	36	0.092	Switzerland
CHL028	5	7	7	0.018	Chile
GEO001	5		5	0.013	Georgia
ROM023	5		5	0.013	Romania
AUT001	4		4	0.010	Austria
AUT025	4		4	0.010	Austria
BEL002	3		3	0.008	Belgium
CUB251	3		3	0.008	Cuba
ECU167	3		3	0.008	Ecuador
ESP172	3		3	0.008	Spain
GUY021	3		3	0.008	Guyana
MEX208	3		3	0.008	Mexico
MWI041	3		3	0.008	Malawi
ITA368	2		2	0.005	Italy
SVK001	2		2	0.005	Slovakia
UGA132	2		2	0.005	Uganda
UKR081	2		2	0.005	Ukraine
AZE004	1		1	0.003	Azerbaijan
ETH013	1		1	0.003	Ethiopia
ETH085	1		1	0.003	Ethiopia
ITA391	1		1	0.003	Italy
MDA011	1		1	0.003	Republic of Moldova
MMR015	1		1	0.003	Myanmar
NER001	1		1	0.003	Niger
UKR023	1		1	0.003	Ukraine
Total	**29,297**	**16,595**	**39,296**	**100**	**World**

APPENDIX XI. *CUCURBITA* TAXA AND CORRESPONDING NUMBER OF ACCESSIONS[3] CONSERVED GLOBALLY

Based on data from Genesys (December 2020), WIEWS (December 2020) and USDA-GRIN (March 2020).

Taxon	Accessions	Biological Status
Cucurbita pepo L.	6,809	Cultivated
Cucurbita pepo subsp. *pepo* L.	367	Cultivated and Wild
Cucurbita pepo var. *ovifera* (L.) Harz (Syn. *Cucurbita pepo* L. *subsp. ovifera var. ovifera*)	107	Cultivated
Cucurbita pepo var. *ozarkana* D. S. Decker	43	Wild
Cucurbita pepo var. *texana* (Scheele) Filov	38	Wild
Cucurbita pepo subsp. *ovifera* (L.) D. S. Decker	30	Wild
Cucurbita pepo subsp. *fraterna* (L. H. Bailey) Lira et al.	12	Wild
Cucurbita maxima Duchesne	6,155	Cultivated
Cucurbita maxima subsp. *maxima* Duchesne	344	Cultivated
Cucurbita maxima subsp. *andreana* (Naudin) Filov	9	Wild
Cucurbita argyrosperma C. Huber	682	Cultivated
Cucurbita argyrosperma subsp. *sororia* (L. H. Bailey) L. Merrick & D. M. Bates	119	Wild
Cucurbita argyrosperma var. *palmeri* (L. H. Bailey) L. Merrick & D. M. Bates	52	Feral
Cucurbita argyrosperma subsp. *argyrosperma* C. Huber	31	Cultivated
Cucurbita argyrosperma var. *callicarpa* L. Merrick & D. M. Bates	17	Cultivated
Cucurbita argyrosperma var. *argyrosperma* C. Huber	15	Cultivated
Cucurbita argyrosperma var. *stenosperma* (Pangalo) L. Merrick & D. M. Bates	14	Cultivated
Cucurbita moschata Duchesne	9,683	Cultivated
Cucurbita ficifolia Bouche	662	Cultivated
Cucurbita sp.	4,357	Mostly Cultivated
Cucurbita foetidissima Kunth	121	Wild
Cucurbita okeechobeensis subsp. *martinezii* (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker	47	Wild
Cucurbita lundelliana L. H. Bailey	42	Wild
Cucurbita palmata S. Watson	33	Wild
Cucurbita digitata A. Gray	22	Wild
Cucurbita ecuadorensis H. C. Cutler & Whitaker	21	Wild
Cucurbita pedatifolia L. H. Bailey	16	Wild
Cucurbita hybr.	11	
Cucurbita okeechobeensis subsp. *okeechobeensis* (Small) L. H. Bailey	9	Wild
Cucurbita okeechobeensis (Small) L. H. Bailey	6	Wild
Cucurbita cordata S. Watson	4	Wild
Cucurbita radicans Naudin	4	Wild
Cucurbita x scabridifolia L. H. Bailey	3	Wild
Total	**29,885**	**Wild and Cultivated**

[3]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

APPENDIX XII. MAJOR HOLDING INSTITUTES AND NUMBER OF ACCESSIONS[4] OF *CUCURBITA*

According to data from WIEWS (December 2020), Genesys (December 2020) and USDA-GRIN (March 2020) and the strategy survey responses.

Holding Institute	Databases	Survey	Databases and survey	% of total	Country or area
RUS001	0	2,992	2,992	8.389	Russian Federation
BRA012	2,888	0	2,888	8.098	Brazil
CRI001	2,119	0	2,119	5.941	Costa Rica
CHN001	0	1,420	1,420	3.981	China
BRA003	1,686	0	1,686	4.727	Brazil
USA016	1,359	0	1,359	3.810	United States of America
USA974	1,219	0	1,219	3.418	United States of America
BRA017	1,124	0	1,124	3.152	Brazil
TWN001	1,115	0	1,115	3.126	Taiwan
HUN003	1,088	0	1,088	3.051	Hungary
DEU146	1,066	0	1,066	2.989	Germany
USA020	1,000	0	1,000	2.804	United States of America
JPN183	863	0	863	2.420	Japan
ESP027	851	0	851	2.386	Spain
USA003	841	0	841	2.358	United States of America
ESP026	810	0	810	2.271	Spain
PRT001	782	782	782	2.193	Portugal
ARG013	0	776	776	2.176	Argentina
ZMB048	777	0	777	2.179	Zambia
ZAF062	677	0	677	1.898	South Africa
POL003	629	0	629	1.764	Poland
CZE122	617	0	617	1.730	Czechia
UZB006	0	589	589	1.651	Uzbekistan
BGR001	580	0	580	1.626	Bulgaria
MEX006	445	0	445	1.248	Mexico
BGD003	444	0	444	1.245	Bangladesh
BOL317	431	0	431	1.208	Bolivia (Plurinational State of)
BRA020	420	0	420	1.178	Brazil
KEN212	404	0	404	1.133	Kenya
TZA016	353	0	353	0.990	United Republic of Tanzania
ROM007	306	364	364	1.021	Romania
ZMB030	262	0	262	0.735	Zambia
MEX194	258	0	258	0.723	Mexico
LSO015	252	0	252	0.707	Lesotho
USA005	245	0	245	0.687	United States of America
IND001	242	245	245	0.687	India
MEX208	202	0	202	0.566	Mexico
MWI041	196	0	196	0.550	Malawi
COL017	174	0	174	0.488	Colombia
ECU023	163	0	163	0.457	Ecuador
PAK001	163	0	163	0.457	Pakistan

[4]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

Holding Institute	Databases	Survey	Databases and survey	% of total	Country or area
UKR048	160	0	160	0.449	Ukraine
MEX263	158	0	158	0.443	Mexico
CHL028	157	92	92	0.258	Chile
MEX201	156	0	156	0.437	Mexico
SDN002	140	0	140	0.393	Sudan
UKR021	137	0	137	0.384	Ukraine
BGD206	133	0	133	0.373	Bangladesh
ARM059	128	0	128	0.359	Armenia
UKR025	125	0	125	0.350	Ukraine
ARG1342	112	0	112	0.314	Argentina
ESP172	112	0	112	0.314	Spain
ETH085	88	0	88	0.247	Ethiopia
MEX131	62	0	62	0.174	Mexico
PRT102	54	0	54	0.151	Portugal
ISR002	51	0	51	0.143	Israel
PRT025	51	0	51	0.143	Portugal
ROM023	51	0	51	0.143	Romania
ARE003	50	0	50	0.140	United Arab Emirates
UKR008	45	0	45	0.126	Ukraine
JOR015	42	0	42	0.118	Jordan
JOR105	42	0	42	0.118	Jordan
USA955	40	0	40	0.112	United States of America
AUT046	39	0	39	0.109	Austria
ITA363	38	0	38	0.107	Italy
CUB005	37	0	37	0.104	Cuba
CUB014	33	0	33	0.093	Cuba
TUN029	33	0	33	0.093	Tunisia
NAM006	30	0	30	0.084	Namibia
GRC005	28	0	28	0.079	Greece
UGA132	28	0	28	0.079	Uganda
PER034	27	0	27	0.076	Peru
USA158	26	0	26	0.073	United States of America
CAN004	25	0	25	0.070	Canada
SWZ015	22	0	22	0.062	Eswatini
BWA015	21	0	21	0.059	Botswana
GBR017	20	0	20	0.056	United Kingdom of Great Britain and Northern Ireland
MEX069	20	0	20	0.056	Mexico
GBR004	19	0	19	0.053	United Kingdom of Great Britain and Northern Ireland
ITA391	18	0	18	0.050	Italy
LKA036	18	0	18	0.050	Sri Lanka
GBR006	16	0	16	0.045	United Kingdom of Great Britain and Northern Ireland
NER001	15	0	15	0.042	Niger
ARM005	14	0	14	0.039	Armenia
MKD001	14	0	14	0.039	North Macedonia
ITA392	13	0	13	0.036	Italy
BGD215	11	0	11	0.031	Bangladesh
ROM019	11	0	11	0.031	Romania
ESP003	10	0	10	0.028	Spain

Holding Institute	Databases	Survey	Databases and survey	% of total	Country or area
ITA393	10	0	10	0.028	Italy
TTO010	9	0	9	0.025	Trinidad and Tobago
ALB026	8	0	8	0.022	Albania
AUT025	8	0	8	0.022	Austria
AZE015	8	0	8	0.022	Azerbaijan
ESP133	8	0	8	0.022	Spain
ESP200	8	0	8	0.022	Spain
TUR001	8	0	8	0.022	Turkey
LBN002	6	0	6	0.017	Lebanon
SWE054	6	6	6	0.017	Sweden
AUT001	5	0	5	0.014	Austria
BLR011	5	0	5	0.014	Belarus
GUY021	5	0	5	0.014	Guyana
THA300	5	0	5	0.014	Thailand
AZE005	4	0	4	0.011	Azerbaijan
BEL002	4	0	4	0.011	Belgium
CHE001	4	11	11	0.031	Switzerland
CUB251	4	0	4	0.011	Cuba
GEO001	4	0	4	0.011	Georgia
MNG030	4	0	4	0.011	Mongolia
URY003	4	0	4	0.011	Uruguay
AZE014	3	0	3	0.008	Azerbaijan
LBY006	3	0	3	0.008	Libya
AUT047	2	0	2	0.006	Austria
AZE004	2	0	2	0.006	Azerbaijan
ECU167	2	0	2	0.006	Ecuador
ESP198	2	0	2	0.006	Spain
HRV041	2	0	2	0.006	Croatia
HRV053	2	0	2	0.006	Croatia
EGY087	1	0	1	0.003	Egypt
ESP004	1	0	1	0.003	Spain
ITA368	1	0	1	0.003	Italy
ITA394	1	0	1	0.003	Italy
LBN020	1	0	1	0.003	Lebanon
MDA011	1	0	1	0.003	Republic of Moldova
SVK001	1	0	1	0.003	Slovakia
UKR012	1	0	1	0.003	Ukraine
UKR023	1	0	1	0.003	Ukraine
World	**29,885**	**7,277**	**35,665**	**100.000**	

APPENDIX XIII. NUMBER OF ACCESSIONS[5] OF *CITRULLUS* BY HOLDING INSTITUTE

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020) and strategy survey responses.

INSTCODE	Databases	Survey	Survey and Databases	% of Total	Country or Area
RUS001		3,154	3,154	22.76	Russian Federation
USA016	1,910		1,910	13.78	United States of America
BRA017	996		996	7.19	Brazil
JPN183	792		792	5.72	Japan
UZB006		574	574	4.14	Uzbekistan
CHN001		568	568	4.10	China
ZAF062	515		515	3.72	South Africa
SDN002	471		471	3.40	Sudan
IND001	449	449	449	3.24	India
BRA003	320		320	2.31	Brazil
USA974	298		298	2.15	United States of America
HUN003	253		253	1.83	Hungary
UKR048	247		247	1.78	Ukraine
BGR001	237		237	1.71	Bulgaria
BRA012		220	220	1.59	Brazil
ESP027	220		220	1.59	Spain
MNG030	200		200	1.44	Mongolia
ESP026	196		196	1.41	Spain
BWA015	184		184	1.33	Botswana
TZA016	149		149	1.08	United Republic of Tanzania
UKR021	124		124	0.89	Ukraine
ARM059	117		117	0.84	Armenia
ZMB048	114		114	0.82	Zambia
MWI041	111		111	0.80	Armenia
POL003	101		101	0.73	Poland
PAK001	90		90	0.65	Pakistan
ARG013		76	76	0.55	Argentina
ZMB030	76		76	0.55	Zambia
ITA004	71		71	0.51	Italy
ITA436	71		71	0.51	Italy
NAM006	71		71	0.51	Namibia
UKR025	65		65	0.47	Ukraine
PRT001	62		62	0.45	Portugal
TWN001	57		57	0.41	Taiwan
TUR001	56		56	0.40	Turkey
BRA020	47		47	0.34	Brazil
ROM021	47		47	0.34	Romania
DEU146	42		42	0.30	Gerrmany
TUN029	40		40	0.29	Tunisia
GBR004	38		38	0.27	United Kingdom of Great Britain and Northern Ireland
ARE003	34		34	0.25	United Arab Emirates
USA158	30		30	0.22	United States of America
KEN212	25		25	0.18	Kenya
AZE015	24		24	0.17	Azerbaijan

[5]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

INSTCODE	Databases	Survey	Survey and Databases	% of Total	Country or Area
ISR002	21		21	0.15	Israel
AZE005	19		19	0.14	Azerbaijan
BOL317	18		18	0.13	Bolivia
ROM007	17		17	0.12	Romania
UKR008	17		17	0.12	Ukraine
ROM019	16		16	0.12	Romania
ESP200	15		15	0.11	Spain
CAN004	14		14	0.10	Canada
JOR015	14		14	0.10	Jordan
LBY006	12		12	0.09	Libya
LSO015	12		12	0.09	Lesotho
GBR006	11		11	0.08	United Kingdom of Great Britain and Northern Ireland
JOR105	10		10	0.07	Jordan
CRI001	9		9	0.06	Costa Rica
SVK001	9		9	0.06	Slovakia
USA005	9		9	0.06	United States of America
SWZ015	8		8	0.06	Eswatini
USA995	8		8	0.06	United States of America
CZE122	6		6	0.04	Mexico
MEX208	6		6	0.04	Mexico
CHL028	5		5	0.04	Chile
ESP003	5		5	0.04	Spain
LBN002	4		4	0.03	Lebanon
PRT102	4		4	0.03	Portugal
ARG1342	3		3	0.02	Argentina
ARM005	3		3	0.02	Armenia
CUB014	3		3	0.02	Cuba
CYP004	3		3	0.02	Cyprus
ESP172	3		3	0.02	Spain
ITA363	3		3	0.02	Italy
MKD001	3		3	0.02	North Macedonia
ARM008	2		2	0.01	Armenia
ARM035	2		2	0.01	Armenia
AZE014	2		2	0.01	Azerbaijan
ESP198	2		2	0.01	Spain
ETH013	2		2	0.01	Ethiopia
GEO001	2		2	0.01	Georgia
ITA393	2		2	0.01	Italy
LKA036	2		2	0.01	Sri Lanka
AZE004	1		1	0.01	Azerbaijan
ECU023	1		1	0.01	Ecuador
GUY021	1		1	0.01	Guyana
HRV044	1		1	0.01	Italy
ITA391	1		1	0.01	Italy
ITA392	1		1	0.01	Italy
ITA435	1		1	0.01	Italy
THA300	1		1	0.01	Thailand
Total	9,264	5,041	13,856	100.00	

APPENDIX XIV. ACCESSIONS[6] OF *LUFFA* BY HOLDING INSTITUTE

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020).

Holding Institute	Accessions	% of Total	Country or Area
TWN001	871	26.563	Taiwan
IND001	701	21.378	India
BGD206	478	14.578	Bangladesh
BGD003	355	10.826	Bangladesh
USA016	167	5.093	USA
BRA003	144	4.392	Brazil
JPN183	134	4.087	Japan
PAK001	119	3.629	Pakistan
MMR015	47	1.433	Myanmar
KEN212	37	1.128	Kenya
LKA036	28	0.854	Sri Lanka
BRA020	26	0.793	Brazil
DEU146	24	0.732	Germany
CZE122	16	0.488	Czech Republic
ESP027	15	0.457	Spain
TZA016	13	0.396	Tanzania
ZMB048	13	0.396	Zambia
GBR004	11	0.335	UK
THA300	9	0.274	Thailand
BGD215	7	0.213	Bangladesh
BGR001	7	0.213	Bulgaria
ESP026	6	0.183	Spain
CRI001	4	0.122	Costa Rica
ESP200	4	0.122	Spain
HUN003	3	0.091	Hungary
AUS165	2	0.061	Australia
AUT025	2	0.061	Austria

Holding Institute	Accessions	% of Total	Country or Area
GUY021	2	0.061	Guyana
MDA011	2	0.061	Moldova
MEX208	2	0.061	Mexico
PHL180	2	0.061	Philippines
PRT001	2	0.061	Portugal
PRT102	2	0.061	Portugal
SWZ015	2	0.061	Swaziland
TTO010	2	0.061	Trinidad and Tobago
UKR008	2	0.061	Ukraine
UKR036	2	0.061	Ukraine
USA974	2	0.061	USA
BEL002	1	0.030	Belgium
CUB014	1	0.030	Cuba
ECU167	1	0.030	Ecuador
ECU308	1	0.030	Ecuador
ETH085	1	0.030	Ethiopia
ISR002	1	0.030	Israel
NAM006	1	0.030	Namibia
POL003	1	0.030	Poland
ROM007	1	0.030	Romania
UGA132	1	0.030	Uganda
UKR021	1	0.030	Ukraine
UKR048	1	0.030	Ukraine
USA005	1	0.030	USA
ZAF062	1	0.030	South Africa
Total	**3,279**	**100**	**World**

[6]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

APPENDIX XV. ACCESSIONS OF *BENINCASA* BY HOLDING INSTITUTE

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020) and strategy survey responses.

Holding Institute	Database	Survey	Databases and Survey	% of Total	Country
TWN001	315		315	19.091	Taiwan
CHN001		300	300	18.182	China
IND001	270		270	16.364	India
JPN183	261		261	15.818	Japan
BGD206	172		172	10.424	Bangladesh
BGD003	151		151	9.152	Bangladesh
PAK001	33		33	2.000	Pakistan
USA003	31		31	1.879	USA
USA016	31		31	1.879	USA
RUS001		30	30	1.818	Russia
DEU146	13		13	0.788	Germany
THA300	10		10	0.606	Thailand
HUN003	9		9	0.545	Hungary
CZE122	6		6	0.364	Czechia
URY003	3		3	0.182	Uruguay
USA974	3		3	0.182	USA
AUT025	2		2	0.121	Austria
CRI001	2		2	0.121	Costa Rica
LKA036	2		2	0.121	Sri Lanka
POL003	2		2	0.121	Poland
BEL002	1		1	0.061	Belgium
CAN004	1		1	0.061	Canada
PHL180	1		1	0.061	Philippines
UKR021	1		1	0.061	Ukraine
Total	**1,320**	**330**	**1,650**	**100**	**World**

APPENDIX XVI. ACCESSIONS[7] OF *LAGENARIA* BY HOLDING INSTITUTE

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020) and strategy survey responses.

Holding Institute	Databases	Survey	Database and Survey	% of Total	Country or Area
USA016	900		900	15.704	United States of America
IND001	743		743	12.965	India
KEN212	478		478	8.341	Kenya
CHN001		370	370	6.456	China
ZAF062	350		350	6.107	South Africa
TWN001	346		346	6.037	Taiwan
BGD206	345		345	6.020	Bangladesh
BGD003	279		279	4.868	Bangladesh
BRA003	277		277	4.833	Brazil
RUS001		266	266	4.641	Russian Federation
TZA016	192		192	3.350	United Republic of Tanzania
JPN183	174		174	3.036	Japan
CRI001	148		148	2.582	Costa Rica
ZMB030	108		108	1.884	Zambia
DEU146	74		74	1.291	Germany
BRA020	67		67	1.169	Brazil
ESP027	55		55	0.960	Spain
HUN003	40		40	0.698	Hungary
ESP026	39		39	0.681	Spain
MWI041	37		37	0.646	Malawi
SDN002	36		36	0.628	Sudan
MMR015	33		33	0.576	Myanmar
PRT001	32		32	0.558	Portugal
SWZ015	32		32	0.558	Eswatini
ZMB048	32		32	0.558	Zambia
NAM006	30		30	0.523	Namibia
BWA015	24		24	0.419	Botswana
USA005	23		23	0.401	United States of America
BGR001	22		22	0.384	Bulgaria
ETH085	18		18	0.314	Ethiopia
PAK001	18		18	0.314	Pakistan
MEX006	15		15	0.262	Mexico
AUS165	14		14	0.244	Australia
GBR004	12		12	0.209	United Kingdom of Great Britain and Northern Ireland
BGD215	10		10	0.174	Bangladesh
BOL317	9		9	0.157	Bolivia (Plurinational State of)
CZE122	8		8	0.140	Czechia
LKA036	7		7	0.122	Sri Lanka
ARG1342	6		6	0.105	Argentina
LSO015	6		6	0.105	Lesotho
MKD001	6		6	0.105	North Macedonia

[7]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

Holding Institute	Databases	Survey	Database and Survey	% of Total	Country or Area
MEX208	5		5	0.087	Mexico
TTO010	4		4	0.070	Trinidad and Tobago
AUT046	3		3	0.052	Austria
ESP172	3		3	0.052	Spain
GBR017	3		3	0.052	United Kingdom of Great Britain and Northern Ireland
THA300	3		3	0.052	Thailand
TUR001	3		3	0.052	Turkey
UKR021	3		3	0.052	Ukraine
ECU023	2		2	0.035	Ecuador
MDA011	2		2	0.035	Republic of Moldova
PHL180	2		2	0.035	Philippines
PRT025	2		2	0.035	Portugal
UKR048	2		2	0.035	Ukraine
AZE014	1		1	0.017	Azerbaijan
CHL028	1		1	0.017	Chile
CYP004	1		1	0.017	Cyprus
GUY021	1		1	0.017	Guyana
ITA363	1		1	0.017	Italy
ITA393	1		1	0.017	Italy
JOR015	1		1	0.017	Jordan
JOR105	1		1	0.017	Jordan
LBY006	1		1	0.017	Libya
POL003	1		1	0.017	Poland
PRT102	1		1	0.017	Portugal
ROM007	1		1	0.017	Romania
USA974	1		1	0.017	United States of America
Total	**5,095**	**636**	**5,731**	**100.000**	**World**

APPENDIX XVII. ACCESSIONS[7] OF *MOMORDICA* BY HOLDING INSTITUTE

According to data from WIEWS (February 2020), Genesys (February 2020) and USDA-GRIN (March 2020) and strategy survey responses.

Holding Institute	Databases	Survey	Databases and Survey	% of Total	Country or Area
BGD206	814		814	26.900	Bangladesh
IND001	564	584	584	19.299	India
TWN001	424	622	622	20.555	Taiwan
JPN183	383		383	12.657	Japan
CHN001		200	200	6.609	China
BGD003	121		121	3.999	Bangladesh
USA016	76	37	37	1.223	United States of America
PAK001	61		61	2.016	Pakistan
KEN212	31		31	1.024	Kenya
GBR004	27		27	0.892	United Kingdom of Great Britain and Northern Ireland
ZAF062	25		25	0.826	South Africa
RUS001		14	14	0.463	Russia
BRA020	11		11	0.364	Brazil
CRI001	9		9	0.297	Costa Rica
USA974	8		8	0.264	United States of America
AUS165	7		7	0.231	Australia
BGD215	7		7	0.231	Bangladesh
GUY021	7		7	0.231	Guyana
SWZ015	7		7	0.231	Eswatini
DEU146	5	5	5	0.165	Germany
ISR002	5		5	0.165	Israel
HUN003	4		4	0.132	Hungary
ZMB048	4		4	0.132	Zambia
CZE122	3		3	0.099	Czechia
LKA036	3		3	0.099	Sri Lanka
MMR015	3		3	0.099	Myanmar
ESP003	2		2	0.066	Spain
MDA011	2		2	0.066	Republic of Moldova
MDG002	2		2	0.066	Madagascar
NPL069	2		2	0.066	Nepal
TTO010	2		2	0.066	Trinidad and Tobago
USA005	2		2	0.066	United States of America
AUT025	1		1	0.033	Austria
BRA003	1		1	0.033	Brazil
BWA015	1		1	0.033	Botswana
CUB014	1		1	0.033	Cuba
ESP026	1		1	0.033	Spain
ETH085	1		1	0.033	Ethiopia
JOR015	1		1	0.033	Jordan
JOR105	1		1	0.033	Jordan
PHL180	1		1	0.033	Philippines
ROM007	1		1	0.033	Romania
UKR048	1		1	0.033	Ukraine
USA047	1		1	0.033	United States of America
Total	**2,633**	**1,462**	**3,026**	**100.000**	**World**

[7]Duplicate accessions that were possible to identify by using DONORNUMB and DONORCODE information from passport data were not counted. However, the majority of duplicates cannot be identified in this way, as in many cases this information is not recorded in passport data.

APPENDIX XVIII. TAXA STANDARDIZATION CONDUCTED TO ANALYZE DATA FROM GENESYS, WIEWS AND USDA-GRIN

Cucumis:

Taxa as Found in Databases	Standardized Taxa
Cucumis	Cucumis sp.
Cucumis aculeatus	Cucumis aculeatus Cogn.
Cucumis africanus	Cucumis africanus L. f.
Cucumis anguria	Cucumis anguria L.
Cucumis anguria subsp. anguria	Cucumis anguria var. anguria
Cucumis anguria subsp. longipes	Cucumis anguria var. anguria
Cucumis anguria var. anguria	Cucumis anguria var. anguria
Cucumis anguria var. longaculeatus	Cucumis anguria var. longaculeatus J. H. Kirkbr.
Cucumis argenteus	Cucumis argenteus (Domin) P. Sebastian & I. Telford
Cucumis asper	Cucumis asper Cogn.
Cucumis callosus	Cucumis callosus Cogn.
Cucumis dinteri	Cucumis sagittatus Peyr.
Cucumis dipsaceus	Cucumis dipsaceus Ehrenb. ex Spach
Cucumis esculentus	Cucumis esculentus Salisb.
Cucumis ficifolia	Cucumis ficifolius A. Rich.
Cucumis ficifolius	Cucumis ficifolius A. Rich.
Cucumis figarei	Cucumis pustulatus Hook. f.
Cucumis flexuosus	Cucumis melo L. group Flexuosus
Cucumis globosus	Cucumis globosus C. Jeffrey
Cucumis hardwickii	Cucumis sativus var. hardwickii (Royle) Alef.
Cucumis heptadactylus	Cucumis heptadactylus Naudin
Cucumis hirsutus	Cucumis hirsutus Sond.
Cucumis humifructus	Cucumis humifructus Stent
Cucumis hystrix	Cucumis hystrix Chakrav.
Cucumis javanicus	Cucumis javanicus (Miq.) Ghebret. & Thulin
Cucumis kalahariensis	Cucumis kalahariensis A. Meeuse
Cucumis leiospermus	Cucumis leiospermus (Wight & Arn.) Ghebret. & Thulin
Cucumis maderaspatanus	Cucumis maderaspatanus L.
Cucumis maxima	Cucumis
Cucumis meeusei	Cucumis meeusei C. Jeffrey
Cucumis melo	Cucumis melo L.
Cucumis melo agrestis	Cucumis melo subsp. agrestis (Naudin) Pangalo
Cucumis melo cantalupensis	Cucumis melo L. group Cantalupensis
Cucumis melo convar. adana	Cucumis melo L.
Cucumis melo convar. cantalupa	Cucumis melo subsp. melo L.
Cucumis melo convar. europens	Cucumis melo L.
Cucumis melo convar. melo	Cucumis melo subsp. melo L.
Cucumis melo gr. agrestis	Cucumis melo L.
Cucumis melo gr. cantalupensis	Cucumis melo L. group Cantalupensis
Cucumis melo gr. cantalupensis sgr. Charentais	Cucumis melo L. group Cantalupensis
Cucumis melo gr. cantalupensis sgr. Prescott	Cucumis melo L. group Cantalupensis
Cucumis melo gr. cantalupensis sgr. Saccharinus	Cucumis melo L. group Cantalupensis
Cucumis melo gr. chito	Cucumis melo L. group Chito
Cucumis melo gr. ibericus	Cucumis melo L. group Ibericus

Taxa as Found in Databases	Standardized Taxa
Cucumis melo gr. ibericus sgr. Amarillo	Cucumis melo L. group Ibericus
Cucumis melo gr. ibericus sgr. Rochet	Cucumis melo L. group Ibericus
Cucumis melo gr. ibericus sgr. Tendral	Cucumis melo L. group Ibericus
Cucumis melo gr. inodorus sgr. Honeydew	Cucumis melo L. group Inodorus
Cucumis melo gr. kachri	Cucumis melo L. group Kachri
Cucumis melo L.	Cucumis melo L.
Cucumis melo melo	Cucumis melo subsp. melo L.
Cucumis melo melo var. commom	Cucumis melo L. group Conomon
Cucumis melo reticulatus	Cucumis melo L. group Cantalupensis
Cucumis melo subsp. agrestis	Cucumis melo subsp. agrestis (Naudin) Pangalo
Cucumis melo subsp. agrestis convar. conomon	Cucumis melo L. group Conomon
Cucumis melo subsp. agrestis var. conomon	Cucumis melo L. group Conomon
Cucumis melo subsp. ameri	Cucumis melo L. group Ameri
Cucumis melo subsp. aqrestis	Cucumis melo subsp. agrestis (Naudin) Pangalo
Cucumis melo subsp. europaeus convar. europae	Cucumis melo L.
Cucumis melo subsp. europaeus var. rokkiford	Cucumis melo L.
Cucumis melo subsp. melo	Cucumis melo subsp. melo L.
Cucumis melo subsp. melo convar. dudaim	Cucumis melo L. group Dudaim
Cucumis melo subsp. melo convar. melo	Cucumis melo subsp. melo L.
Cucumis melo subsp. melo f. cantalupensis	Cucumis melo L. group Cantalupensis
Cucumis melo subsp. melo f. cantalupensis gr. charentais	Cucumis melo L. group Cantalupensis
Cucumis melo subsp. melo f. inodorus gr. canari	Cucumis melo L. group Inodorus
Cucumis melo subsp. melo f. inodorus gr. honeydew	Cucumis melo L. group Inodorus
Cucumis melo subsp. melo f. inodorus gr. rochet	Cucumis melo L. group Inodorus
Cucumis melo subsp. melo f. inodorus gr. tendral	Cucumis melo L. group Inodorus
Cucumis melo subsp. melo f. reticulatus	Cucumis melo L. group Cantalupensis
Cucumis melo subsp. melo var. flexuosus	Cucumis melo L. group Flexuosus
Cucumis melo subsp. microcarpus	Cucumis melo subsp. melo L.
Cucumis melo subsp. orientalis	Cucumis melo subsp. orientale Sageret ex Filov
Cucumis melo subsp. rigida var. ameri	Cucumis melo L.
Cucumis melo subsp. zard	Cucumis melo L.
Cucumis melo var cantalupensis	Cucumis melo L. group Cantalupensis
Cucumis melo var. aegyptiacus	Cucumis melo L.
Cucumis melo var. agrestis	Cucumis melo var. agrestis Naudin
Cucumis melo var. anguria	Cucumis melo L.
Cucumis melo var. anguria, longipes	Cucumis melo L.
Cucumis melo var. cantalupensis	Cucumis melo L. group Cantalupensis
Cucumis melo var. cantalupo	Cucumis melo L. group Cantalupensis
Cucumis melo var. chito	Cucumis melo L. group Chito
Cucumis melo var. conomon	Cucumis melo L. group Conomon
Cucumis melo var. cultus	Cucumis melo var. cultus Kurz
Cucumis melo var. dudame	Cucumis melo L. group Chito
Cucumis melo var. flexuosus	Cucumis melo L. group Flexuosus
Cucumis melo var. inodorus	Cucumis melo L. group Inodorus
Cucumis melo var. makuwa	Cucumis melo L. group Makuwa
Cucumis melo var. Melo	Cucumis melo L.
Cucumis melo var. momordica	Cucumis melo L. group Momordica
Cucumis melo var. phoetidissima	Cucumis melo L.
Cucumis melo var. praecox	Cucumis melo L.
Cucumis melo var. reticulatus	Cucumis melo L. group Cantalupensis

Taxa as Found in Databases	Standardized Taxa
Cucumis melo var. texanus	Cucumis melo var. texanus Naudin
Cucumis melo var. utilissimus	Cucumis melo L. group Conomon
Cucumis melo var.bucharici	Cucumis melo L.
Cucumis melo var.cassaba	Cucumis melo L. group Cassaba
Cucumis melo var.reticulatus	Cucumis melo L. group Cantalupensis
Cucumis metulifer	Cucumis metuliferus E. Mey. ex Naudin
Cucumis metuliferus	Cucumis metuliferus E. Mey. ex Naudin
Cucumis momordica	Cucumis melo L. group Momordica
Cucumis muriculatus	Cucumis muriculatus Chakrav.
Cucumis myriocarpus	Cucumis myriocarpus Naudin
Cucumis myriocarpus leptodermis	Cucumis myriocarpus subsp. leptodermis (Schweick.) C. Jeffrey & P. Halliday
Cucumis myriocarpus subsp. leptodermis	Cucumis myriocarpus subsp. leptodermis (Schweick.) C. Jeffrey & P. Halliday
Cucumis myriocarpus subsp. myriocarpus	Cucumis myriocarpus subsp. myriocarpus Naudin
Cucumis prophetarum	Cucumis prophetarum L.
Cucumis prophetarum subsp. dissectus	Cucumis prophetarum subsp. dissectus (Naudin) C. Jeffrey
Cucumis prophetarum subsp. prophetarum	Cucumis prophetarum subsp. prophetarum L.
Cucumis pustulatus	Cucumis pustulatus Hook. f.
Cucumis quintanilhae	Cucumis quintanilhae R. Fern. & A. Fern.
Cucumis rati	Cucumis
Cucumis sacleuxii	Cucumis sacleuxii Pailleux & Bois
Cucumis sagittatus	Cucumis sagittatus Peyr.
Cucumis sativus	Cucumis sativus L.
Cucumis sativus [Concombre]	Cucumis sativus L.
Cucumis sativus [Cornichon]	Cucumis sativus L.
Cucumis sativus L.	Cucumis sativus L.
Cucumis sativus L. var. piculus Fil.	Cucumis sativus L.
Cucumis sativus L. var. sativus	Cucumis sativus var. sativus
Cucumis sativus subsp. sativus	Cucumis sativus var. sativus
Cucumis sativus var european	Cucumis sativus L.
Cucumis sativus var transcaucasiacum	Cucumis sativus L.
Cucumis sativus var. europeaus	Cucumis sativus var. sativus
Cucumis sativus var. hardwickii	Cucumis sativus var. hardwickii (Royle) Alef.
Cucumis sativus var. hardwickii x Cucumis sativus var. sativus	Cucumis sativus L.
Cucumis sativus var. izmir	Cucumis sativus var. sativus
Cucumis sativus var. sativus	Cucumis sativus var. sativus
Cucumis sativus var. sikkimensis	Cucumis sativus var. sikkimensis Hook. f.
Cucumis sativus var. vulgaris	Cucumis sativus var. sativus
Cucumis sativus var. xishuangbannanesis	Cucumis sativus var. xishuangbannanesis ined.
Cucumis sativus x hardwickii	Cucumis sativus L.
Cucumis setosus	Cucumis setosus Cogn.
Cucumis silentvalleyi	Cucumis silentvalleyi (Manilal et al.) Ghebret. & Thulin
Cucumis sp.	Cucumis sp.
Cucumis sp. nov.	Cucumis
Cucumis spp.	Cucumis sp.
Cucumis subsericeus	Cucumis subsericeus Hook. f.
Cucumis trigonus	Cucumis trigonus Roxb.
Cucumis utilissimus	Cucumis melo L. group Conomon
Cucumis vulgaris	Cucumis vulgaris E.H.L.Krause
Cucumis zambianus	Cucumis zambianus Widrlechner et al.

Taxa as Found in Databases	Standardized Taxa
Cucumis zeyheri	Cucumis zeyheri Sond.
Cucumis zeyheri var. sativus	Cucumis zeyheri Sond.
Cucumus sativus	Cucumis sativus L.

Cucurbita:

Taxon as Found in Databases	Standardized Taxa
Cucurbita	Cucurbita sp.
Cucurbita ???	Cucurbita sp.
Cucurbita andreana	Cucurbita maxima subsp. andreana (Naudin) Filov
Cucurbita argyrosperma	Cucurbita argyrosperma C. Huber
Cucurbita argyrosperma argyrosperma	Cucurbita argyrosperma subsp. argyrosperma C. Huber
Cucurbita argyrosperma sororia	Cucurbita argyrosperma subsp. sororia (L. H. Bailey) L. Merrick & D. M. Bates
Cucurbita argyrosperma subsp. argyrosperma	Cucurbita argyrosperma subsp. argyrosperma C. Huber
Cucurbita argyrosperma subsp. sororia	Cucurbita argyrosperma subsp. sororia (L. H. Bailey) L. Merrick & D. M. Bates
Cucurbita argyrosperma var. argyrosperma	Cucurbita argyrosperma var. argyrosperma C. Huber
Cucurbita argyrosperma var. callicarpa	Cucurbita argyrosperma var. callicarpa L. Merrick & D. M. Bates
Cucurbita argyrosperma var. palmeri	Cucurbita argyrosperma var. palmeri (L. H. Bailey) L. Merrick & D. M. Bates
Cucurbita argyrosperma var. stenosperma	Cucurbita argyrosperma var. stenosperma (Pangalo) L. Merrick & D. M. Bates
Cucurbita argyrospermasororia	Cucurbita argyrosperma subsp. sororia (L. H. Bailey) L. Merrick & D. M. Bates
Cucurbita convar	Cucurbita sp.
Cucurbita cordata	Cucurbita cordata S. Watson
Cucurbita dichotoma	Cucurbita sp.
Cucurbita digitata	Cucurbita digitata A. Gray
Cucurbita ecuadorensis	Cucurbita ecuadorensis H. C. Cutler & Whitaker
Cucurbita faprafolia	Cucurbita sp.
Cucurbita ficifolia	Cucurbita ficifolia Bouche
Cucurbita foetidissima	Cucurbita foetidissima Kunth
Cucurbita hybr.	Cucurbita hybr.
Cucurbita lagenaria	Lagenaria siceraria (Molina) Standl.
Cucurbita lundelliana	Cucurbita lundelliana L. H. Bailey
Cucurbita martinezii	Cucurbita okeechobeensis subsp. martinezii (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker
Cucurbita maxima	Cucurbita maxima Duchesne
Cucurbita maxima convar. bananina	Cucurbita maxima Duchesne
Cucurbita maxima convar. maxima	Cucurbita maxima subsp. maxima Duchesne
Cucurbita maxima Duch. var. maxima	Cucurbita maxima subsp. maxima Duchesne
Cucurbita maxima Duchesne	Cucurbita maxima Duchesne
Cucurbita maxima Duchesne.	Cucurbita maxima Duchesne
Cucurbita maxima subsp. andreana	Cucurbita maxima subsp. andreana (Naudin) Filov
Cucurbita maxima subsp. maxima	Cucurbita maxima subsp. maxima Duchesne
Cucurbita maxima subsp. maxima convar. bananina	Cucurbita maxima Duchesne
Cucurbita maxima subsp. maxima convar. hubbardina	Cucurbita maxima Duchesne
Cucurbita maxima subsp. maxima convar. maxima	Cucurbita maxima Duchesne
Cucurbita maxima subsp. maxima convar. turbanifor	Cucurbita maxima Duchesne
Cucurbita maxima subsp. maxima convar. zapallitin	Cucurbita maxima Duchesne
Cucurbita maxima subsp. maxima var.	Cucurbita maxima subsp. maxima Duchesne
Cucurbita maxima subsp. maxima var. Maxima	Cucurbita maxima subsp. maxima Duchesne
Cucurbita maxima var. hollandrae	Cucurbita maxima Duchesne

Taxon as Found in Databases	Standardized Taxa
Cucurbita maxima var. maxima	Cucurbita maxima subsp. maxima Duchesne
Cucurbita maxima var. turbaniformis	Cucurbita maxima subsp. maxima Duchesne
Cucurbita melanosperma	Cucurbita ficifolia Bouche
Cucurbita mixta	Cucurbita argyrosperma subsp. argyrosperma C. Huber
Cucurbita moschata	Cucurbita moschata Duchesne
Cucurbita moschata convar. moschata	Cucurbita moschata Duchesne
Cucurbita moschata subsp. borealiamerikanika	Cucurbita moschata Duchesne
Cucurbita moschata subsp. maxima var. Maxima	Cucurbita moschata Duchesne
Cucurbita moschata subsp. melo	Cucurbita moschata Duchesne
Cucurbita moschata var. japonica	Cucurbita moschata Duchesne
Cucurbita okeechobeensis	Cucurbita okeechobeensis (Small) L. H. Bailey
Cucurbita okeechobeensis martinezii	Cucurbita okeechobeensis subsp. martinezii (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker
Cucurbita okeechobeensis subsp. martinezii	Cucurbita okeechobeensis subsp. martinezii (L. H. Bailey) T. C. Andres & Nabhan ex T. W. Walters & D. S. Decker
Cucurbita okeechobeensis subsp. okeechobeensis	Cucurbita okeechobeensis subsp. okeechobeensis (Small) L. H. Bailey
Cucurbita ornamental	Cucurbita sp.
Cucurbita palmata	Cucurbita palmata S. Watson
Cucurbita pedatifolia	Cucurbita pedatifolia L. H. Bailey
Cucurbita pepo	Cucurbita pepo L.
Cucurbita pepo .var. oblonga	Cucurbita pepo L.
Cucurbita pepo cMP	Cucurbita pepo L.
Cucurbita pepo convar. girimontia	Cucurbita pepo subsp. pepo L.
Cucurbita pepo convar. giromontia	Cucurbita pepo subsp. pepo L.
Cucurbita pepo convar. giromontiina	Cucurbita pepo subsp. pepo
Cucurbita pepo convar. giromontiina var. zukkin	Cucurbita pepo L.
Cucurbita pepo convar. giromontina	Cucurbita pepo subsp. pepo
Cucurbita pepo convar. microcarpina var. pomifo	Cucurbita pepo L.
Cucurbita pepo convar. patissonia	Cucurbita pepo var. ovifera (L.) Harz
Cucurbita pepo convar. patissonina	Cucurbita pepo L.
Cucurbita pepo convar. patissonina forma radiat	Cucurbita pepo L.
Cucurbita pepo convar. pepo var. pepo	Cucurbita pepo L.
Cucurbita pepo forma obconga	Cucurbita pepo L.
Cucurbita pepo fraterna	Cucurbita pepo subsp. fraterna (L. H. Bailey) Lira et al.
Cucurbita pepo giraumons	Cucurbita pepo subsp. pepo L.
Cucurbita pepo L.	Cucurbita pepo L.
Cucurbita pepo L. var. giaramontis	Cucurbita pepo subsp. pepo L.
Cucurbita pepo L. var. melopepo	Cucurbita pepo var. ovifera (L.) Harz
Cucurbita pepo L. var. pepo Cucurbita pepo L. var. pepo	Cucurbita pepo L.
Cucurbita pepo ovifera	Cucurbita pepo subsp. ovifera (L.) D. S. Decker
Cucurbita pepo pepo	Cucurbita pepo subsp. pepo L.
Cucurbita pepo subsp. brevicaulis var. sorediform	Cucurbita pepo L.
Cucurbita pepo subsp. fraterna	Cucurbita pepo subsp. fraterna (L. H. Bailey) Lira et al.
Cucurbita pepo subsp. ovifera	Cucurbita pepo subsp. ovifera (L.) D. S. Decker
Cucurbita pepo subsp. pepo	Cucurbita pepo subsp. pepo L.
Cucurbita pepo subsp. pepo convar. citrullinina	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. cucumiformis	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. giromontiina	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. giromontiina var. oleifera	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. microcarpina	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. patissonina	Cucurbita pepo L.

Taxon as Found in Databases	Standardized Taxa
Cucurbita pepo subsp. pepo convar. pepo	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. pepo var. ob	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. pepo var. pe	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. pepo var. pepo	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. pepo var. styriaca	Cucurbita pepo L.
Cucurbita pepo subsp. pepo convar. torticollis	Cucurbita pepo L.
Cucurbita pepo subsp. pepo var.	Cucurbita pepo subsp. pepo L.
Cucurbita pepo subsp. pepo var. citriformis	Cucurbita pepo L.
Cucurbita pepo subsp. pepo var. melopepo	Cucurbita pepo L.
Cucurbita pepo subsp. pepo var. oblonga	Cucurbita pepo L.
Cucurbita pepo subsp. pepo var. oleifera	Cucurbita pepo L.
Cucurbita pepo subsp. pepo var. oleiforma	Cucurbita pepo L.
Cucurbita pepo subsp. pepo var. pyxidaris	Cucurbita pepo L.
Cucurbita pepo subsp. texana convar. patissonina	Cucurbita pepo L.
Cucurbita pepo subsp. texana convar. torticollis	Cucurbita pepo L.
Cucurbita pepo var. alba	Cucurbita pepo L.
Cucurbita pepo var. aurantia	Cucurbita pepo L.
Cucurbita pepo var. citrulina	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. citrulina Alef.	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. clypeata	Cucurbita pepo L.
Cucurbita pepo var. condensa	Cucurbita pepo L.
Cucurbita pepo var. cucumiformis	Cucurbita pepo L.
Cucurbita pepo var. giraumonas	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. giraumontia	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. giromontia	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. giromontiina	Cucurbita pepo subsp. pepo
Cucurbita pepo var. maxima	Cucurbita maxima subsp. maxima Duchesne
Cucurbita pepo var. melopepo	Cucurbita pepo var. ovifera (L.) Harz
Cucurbita pepo var. melopepo (	Cucurbita pepo var. ovifera (L.) Harz
Cucurbita pepo var. montia	Cucurbita pepo L.
Cucurbita pepo var. nigra	Cucurbita pepo L.
Cucurbita pepo var. oblonga	Cucurbita pepo L.
Cucurbita pepo var. oleifera	Cucurbita pepo subsp. ovifera (L.) D. S. Decker
Cucurbita pepo var. ovifera	Cucurbita pepo var. ovifera (L.) Harz
Cucurbita pepo var. ozarkana	Cucurbita pepo var. ozarkana D. S. Decker
Cucurbita pepo var. patisoniana	Cucurbita pepo L.
Cucurbita pepo var. pepo	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. piriformis forma minocarpa	Cucurbita pepo L.
Cucurbita pepo var. pomiformis	Cucurbita pepo L.
Cucurbita pepo var. pyxidaris	Cucurbita pepo L.
Cucurbita pepo var. radiata	Cucurbita pepo L.
Cucurbita pepo var. romanica	Cucurbita pepo L.
Cucurbita pepo var. saccharata	Cucurbita pepo L.
Cucurbita pepo var. striata	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. styriaca	Cucurbita pepo subsp. pepo L.
Cucurbita pepo var. texana	Cucurbita pepo var. texana (Scheele) Filov
Cucurbita pepo var. verrucosa	Cucurbita pepo L.
Cucurbita radicans	Cucurbita radicans Naudin
Cucurbita scabridifolia	Cucurbita x scabridifolia L. H. Bailey
Cucurbita sororia	Cucurbita argyrosperma subsp. sororia (L. H. Bailey) L. Merrick & D. M. Bates

Taxon as Found in Databases	Standardized Taxa
Cucurbita sp.	Cucurbita spp.
Cucurbita sp. ornamental	Cucurbita sp.
Cucurbita spp.	Cucurbita spp.
Cucurbita turbaniformis	Cucurbita maxima subsp. maxima Duchesne
Cucurbita x scabridifolia	Cucurbita x scabridifolia L. H. Bailey

Citrullus:

Taxon as Found in Databases	Standardized Taxa
Citrullus	Citrullus sp.
Citrullus aedulus	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus amarus	Citrullus amarus Schrad.
Citrullus colocynthis	Citrullus colocynthis (L.) Schrad.
Citrullus ecirrhosus	Citrullus ecirrhosus Cogn.
Citrullus edulis	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus edulis var. lanatus	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus (Thunb.) Matsumura & Nakai	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus convar. lanatus	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus convar. vulgaris	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus subsp. lanatus (Citroides Group)	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus subsp. lanatus (Lanatus Group)	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus subsp. vulgaris	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus subsp. vulgaris (Dessert Group)	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus subsp. vulgaris var. caffer	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus var. citroides	Citrullus amarus Schrad.
Citrullus lanatus var. lanatus	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus lanatus var. vulgaris	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus mucosospermus	Citrullus mucosospermus (Fursa) Fursa
Citrullus naudinianus	Citrullus naudinianus (Sond.) Hook. f.
Citrullus rehmii	Citrullus rehmii De Winter
Citrullus sp.	Citrullus sp.
Citrullus sp. aff. glandulosa	Citrullus sp.
Citrullus spp.	Citrullus sp.
Citrullus vulgairs	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus vulgaris	Citrullus lanatus (Thunb.) Matsum. & Nakai
Citrullus vulgaris var. citroide	Citrullus amarus Schrad.

Luffa:

Taxon as Found in Databases	Standardised Taxa
Luffa	Luffa sp.
Luffa acutangula	Luffa acutangula (L.) Roxb.
Luffa acutangula f. amara (Roxb.) W.J.de Wilde & Duyfjes	Luffa acutangula var. amara (Roxb.)C.B. Clarke
Luffa acutangula var. amara	Luffa acutangula var. amara (Roxb.)C.B. Clarke
Luffa aegyptiaca	Luffa aegyptiaca Mill.
Luffa aegyptiaca var insularum	Luffa aegyptiaca Mill.
Luffa cylindrica	Luffa aegyptiaca Mill.
Luffa echinata	Luffa echinata Roxb.
Luffa graveolens	Luffa graveolens Roxb.
Luffa hermaphrodita	Luffa acutangula (L.) Roxb.
Luffa Luffa cylindrica	Luffa aegyptiaca Mill.
Luffa operculata	Luffa sepium (G. Mey.) C. Jeffrey
Luffa pedata	Luffa aegyptiaca Mill.

Taxon as Found in Databases	Standardised Taxa
Luffa pentandra	Luffa aegyptiaca Mill.
Luffa saccata	Luffa saccata F.Muell. ex Naudin
Luffa sepium	Luffa sepium (G. Mey.) C. Jeffrey
Luffa sp.	Luffa sp.
Luffa spp.	Luffa sp.
Luffa tuberosa	Momordica cymbalaria Hook. f.

Benincasa:

Taxon as Found in Databases	Standardised Taxa
Benincasa fistulosa	Benincasa fistulosa (Stocks) H. Schaef. & S. S. Renner
Benincasa hispida	Benincasa hispida (Thunb.) Cogn.
Benincasa hispida (Thumberg ex Murray) Cogniaux	Benincasa hispida (Thunb.) Cogn.
Benincasa hispida cogn. var. clavata	Benincasa hispida (Thunb.) Cogn.
Benincasa pruriens f. hispida (Thunb.) W.J.de Wilde & Duyfjes	Benincasa hispida (Thunb.) Cogn.
Benincasa spp.	Benincasa sp.
Lagenaria leucantha var. clavata	Benincasa hispida (Thunb.) Cogn.
Lagenaria siceraria var. hispida	Benincasa hispida (Thunb.) Cogn.

Lagenaria:

Taxon as Found in Databases	Standardised Taxa
Lagenaria	Lagenaria sp.
Lagenaria abyssinica	Lagenaria abyssinica (Hook. f.) C. Jeffrey
Lagenaria breviflora	Lagenaria breviflora (Benth.) Roberty
Lagenaria Lagenaria siceraria	Lagenaria siceraria (Molina) Standl.
Lagenaria leucantha var. clavata	Benincasa hispida (Thunb.) Cogn.
Lagenaria leucantha var. depressa	Lagenaria siceraria (Molina) Standl.
Lagenaria leucantha var. gourda	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria (Md Stand)	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria forma clavata	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria forma gourda	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria subsp. asiatica	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria subsp. siceraria	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria var. depressa	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria var. hispida	Benincasa hispida (Thunb.) Cogn.
Lagenaria siceraria var. siceraria	Lagenaria siceraria (Molina) Standl.
Lagenaria siceraria var. turbinata	Lagenaria siceraria (Molina) Standl.
Lagenaria sp.	Lagenaria sp.

Momordica:

Taxon as Found in Databases	Standardised Taxa
Momordica	Momordica sp.
Momordica anigosantha	Momordica anigosantha Hook.f.
Momordica balsamina	Momordica balsamina L.
Momordica cardiospermoides	Momordica cardiospermoides Klotzsch
Momordica charantia	Momordica charantia L.
Momordica charantia var. muricata	Momordica charantia var. muricata (Willd.) Chakrav.
Momordica clematidea	Momordica clematidea Sond.
Momordica cochinchinensis	Momordica cochinchinensis (Lour.) Spreng.
Momordica dioica	Momordica dioica Roxb. ex Willd.
Momordica foetida	Momordica foetida Schumach.
Momordica involucrata	Momordica involucrata E.Mey.
Momordica Momordica charantia	Momordica sect. Raphanistrocarpus Baill.
Momordica peteri	Momordica peteri A. Zimm.
Momordica repens	Momordica repens Bremek.
Momordica rostrata	Momordica rostrata A. Zimm.
Momordica sahyadrica	Momordica sahyadrica Kattuk. & V. T. Antony
Momordica sp.	Momordica sp.
Momordica spinosa	Momordica spinosa Chiov.
Momordica spp.	Momordica sp.
Momordica subangulata	Momordica subangulata Blume
Momordica subangulata subsp. renigera	Momordica subangulata subsp. renigera (Wall. ex G. Don) W. J. de Wilde
Momordica trifoliolata	Momordica trifoliolata Hook. f.
Momordica tuberosa	Momordica cymbalaria Hook. f.

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