

BRINGING AN HISTORIC COLLECTION INTO THE MODERN ERA: CURATING THE J. K. UNDERWOOD SEED COLLECTION AT THE UNIVERSITY OF TENNESSEE HERBARIUM (TENN)

CHELSEA N. MILLER, HOLLY BRABAZON, IAN M. WARE,
NATHANIEL H. KINGSLEY, AND JESSICA M. BUDKE

*University of Tennessee Herbarium (TENN), Ecology and Evolutionary Biology Department,
University of Tennessee, Knoxville, Tennessee 37996, USA*

Abstract—The University of Tennessee Herbarium (TENN) presents a case study for modernizing an historic seed collection. TENN staff recently rediscovered the J. K. Underwood Seed Collection (ca. 1931–1964), containing over 700 unique specimens, hidden away in storage. We employed a series of curation actions to modernize the collection and render it useful to researchers. This included physically organizing and digitally indexing the collection, updating scientific names to current taxonomy, storing the specimens in modern archival-quality containers, housing the collection in environmentally-controlled conditions, and increasing accessibility of the collection by photographing specimens and integrating these images into our existing website (tenn.bio.utk.edu). Our efforts also included developing a protocol for adding new accessions to the collection and advertising the utility of the collection as a source of morphological data on seeds for identification, research, and teaching. We also review modern strategies for curating seed collections. Specifically, we emphasize the importance of increasing visibility of collections through visual, digital representations. This expands the utility of collections and fosters global information sharing across disciplines. We present our curation project as a case study that can serve as a model for curating historic seed collections.

Key words.—Curation, herbarium, historic, reference collection, seeds.

Associate Editor.—Mariel Campbell

INTRODUCTION

Herbaria are crucial resources for biological research. As physical repositories of botanical specimens, they provide unique opportunities for generating a wide array of scientific data, including morphological, molecular, spatial/occurrence, and life history data from plant species around the world (James et al. 2018). Researchers use these data to construct phylogenies to elucidate evolutionary relationships (Savolainen et al. 1995, Bolmgren and Lonnberg, 2005); build environmental niche models to test correlations between climatic variables and species distributions (Elith and Leathwick 2007, Loiselle et al. 2008); generate genomic data using next-generation sequencing for evolutionary, domestication, and population studies (Staats et al. 2013, Besnard et al. 2014); and calculate species richness and biodiversity indices using locality or elevational range data (Wolf and Alejandro 2003, Bhattarai et al. 2004). Herbarium records are also used to evaluate and identify species at risk of extinction (Schatz 2002), and even discover new species (Bebber et al. 2010). Access to these historical collections and the data contained in them is only continuing to improve with the major strides the community has taken to enter information in databases and to digitize botanical specimens (i.e., CNABH 2018, iDigBio 2018, SERNEC 2018).

Seed collections constitute unique sources of biological and archaeological information. Because DNA has been shown to degenerate more slowly in seeds than vegetative plant material, seed collections are ideal for the analysis of aged and ancient DNA, which has been successfully studied from seeds up to 4,000 years old (Leino et al. 2009). Seed collections, such as the Svalbard Global Seed Vault (2018), provide critical information on the genetic diversity of agriculturally important landraces (Parzies et al. 2000, Ortiz-Garcia et al. 2005) and the comparative performance of obsolete versus current cultivars

(Bridge and Meredith 1983), which are important for archaeological studies and the improvement of crop plants. Other seed collections are devoted to the *ex situ* conservation of wild plant species for reintroduction and restoration work (Millennium Seed Bank 2018). Seed collections housed in herbaria are often used as reference collections for identification, which is a key aspect of many biological and archaeological studies, including efforts to generate accurate botanical inventories for ecosystem assessments (Kitamura et al. 2005), investigations of paleobotanical changes in vegetation (Wadley 2004), tracking the movement of invasive species across the landscape (Chown et al. 2012), ascertaining the diets of birds (Holland et al. 2006) and mammals (Santos et al. 2003), and identifying remains of plants used by humans and the weed floras of ancient crops (Nesbitt et al. 2003).

Although important tools for researchers, herbarium seed collections can be limited in terms of accessibility. Many seed collections have not been photographed or entered into databases and are best explored with an in-person visit. Furthermore, when seed collections are photographed, images can be insufficient for identification. Confident identification often requires the examination of seeds from multiple angles, dissection, and even manipulations to simulate the appearance of field-collected seeds (Nesbitt et al. 2003), thus justifying the continued preservation of physical seeds in reference collections. Improvements in analysis, including z-stacking software that enables specimens with a large depth of field to be imaged entirely in focus and with digital scale bars that can be automatically added for rapid measuring, can yield high-quality photographs that are useful tools for identification. Coupling this with compilations of multiple images of a single specimen, showing detailed aspects from different angles, can assist in identification utility. These images can then be made widely available to researchers located at institutions across the world. They also serve as a digital backup of the specimens and their data in case of physical loss or damage by threats such as the fire in 1934 that resulted in the loss of the entire University of Tennessee–Knoxville Herbarium (White 1981), or the more recent fire in August 2017 at the University of Vermont’s Pringle Herbarium which put a collection of over 300,000 plant specimens at risk (Higgins DeSmet 2017).

This article outlines the actions taken by staff at the University of Tennessee–Knoxville Herbarium (TENN) to bring an historic seed collection out of the storage closet, modernize its curation, promote its use as an identification reference collection, digitize it to mitigate risk of loss and improve the long-term security of the data, and increase its accessibility to remote researchers.

BACKGROUND

TENN is the third largest herbarium in the southeast (Thiers 2018) and currently contains over 600,000 specimens. TENN houses specimens from around the world, specializing in the flora of Tennessee, the southeastern United States of America (USA), Mexico, and Central America. TENN contains 150,000 bryophyte and 90,000 fungal specimens, including over 6,000 plant pathogens, and has the largest collection of specimens from the state of Tennessee. As a repository for specimens from the Great Smoky Mountains National Park (GSMNP), TENN is home to a large collection of specimens serving as a physical showcase of the park’s high floral biodiversity across time. GSMNP boasts more than 1,600 native angiosperms and over 500 native species of nonvascular plants (National Park Service 2018), many of which are represented at TENN.

Recently, new staff members at TENN rediscovered an historic seed collection tucked away in a storage closet. The J. K. Underwood Seed Collection was housed in glass vials with handwritten labels, rolling loose in the drawers of an old map case (Fig. 1). It is a

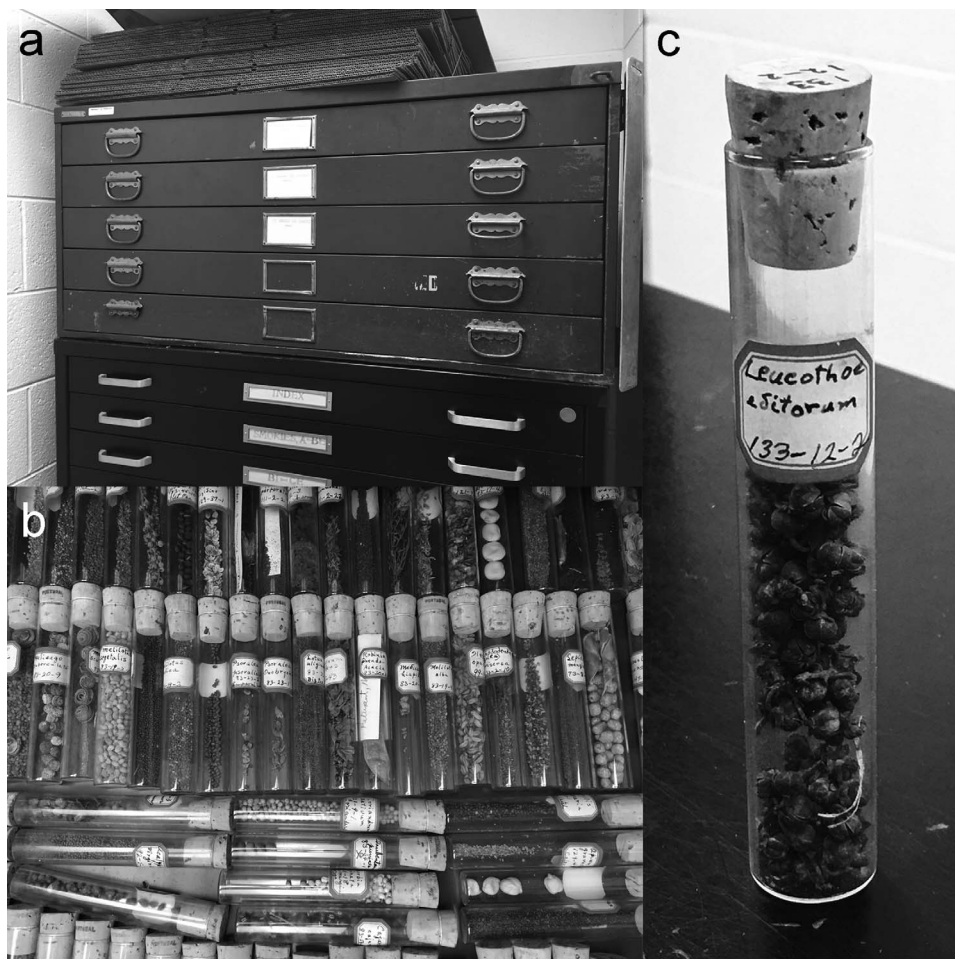


Figure 1. (a) The J. K. Underwood Seed Collection was rediscovered by new staff members in an old map case at TENN. (b) The collection was originally housed rolling loose in map drawers, in glass vials with decaying cork stoppers and handwritten labels. (c) Original glass vials storing specimens of the J. K. Underwood Seed Collection showing handwritten labels that included the specimen's scientific name and a catalog number specific to this historic collection. Labels were difficult to read and on nonarchival paper.

diverse collection containing 716 specimens in 395 genera across 92 families, with many specimens in agronomically important families, such as the Fabaceae (118 species), Asteraceae (87 species), and Poaceae (74 species). Each specimen has a multipart catalog number, but all other metadata, including collection location and date, were not stored with the specimens. Attempts to locate Underwood's collection notebooks were unfortunately not successful. One might wonder why a collection in this state would be preserved. As those familiar with herbaria and museums well know, collections staff often have an intense drive to preserve specimens even when they are in a state of disrepair, with the long-term vision that they might someday be curated and prove useful to future researchers. When new staff at TENN rediscovered the J. K. Underwood Seed Collection, we were inspired to put this vision into action with the help of students and volunteers working at the herbarium.

Judson Kemp Underwood (1898–1975) was a professor of agronomy and plant soil sciences who specialized in forage and turf grasses in the University of Tennessee College of Agricultural Sciences and Natural Resources in Knoxville. He also served as an honorary curator at TENN (Walker 2016). Underwood made many contributions to the botanical sciences during his career, including his work on plant diseases, his campaign to reduce the use of agricultural chemicals, and his efforts in developing a purple-seeded red clover with superior crop/forage characteristics (Smith 1999, Walker 2016). He also published texts on the maintenance and care of Tennessee lawns (Underwood 1955, 1973). Although the metadata associated with the seed collection is missing, our best estimate is that the seeds were collected during Underwood's tenure at the university from 1931–1964.

In 2017, a curation project was undertaken to modernize the J. K. Underwood Seed Collection and render it useful to researchers as a reference collection for seed identification and as a repository of seed morphology. In its original state, use of the collection was nearly impossible. There was a previous inventory of the collection in 2007 thanks to University of Tennessee–Knoxville Curator of Paleoethnobotany, Dr. Gary Crites, but the list was incomplete, and the specimen order was shifted over time due to the loose housing of the specimen vials which rolled around in the drawers. The hand-written labels were also difficult to read and were made of nonarchival paper that had begun to fade and peel. Locating specific taxa was also challenging due to the historic names on the specimens, which were not updated to current taxonomy. The collection was also at risk of degradation due to insects and mold because it was not stored in a sealed cabinet or in an environmentally controlled room. Finally, viewing was made difficult because the vials rolled around when placed under a microscope, so users were forced to remove specimens from the vials to view them, potentially causing damage to the seeds.

This paper presents the actions taken to render the historic J. K. Underwood Seed Collection useful to researchers. Our objectives were to: create an indexed and organized collection; update the names to current taxonomy; create archival-quality herbaria labels; transfer specimens into more accessible and protective containers; and house the collection in environmentally controlled conditions. Our goals also included photographing the collection, uploading the images to the TENN website, and advertising the utility of the collection as a source of morphological data on seeds for identification, research, and teaching. Further, we outline our protocol for expanding the existing collection through the addition of new specimens. Due to the small number of publications focusing on the management of seed collections (Nesbitt et al. 2003), we present our curation project as a case study that can serve as one model for curating historic seed collections.

CURATION PROCESS

Name Resolution and Organization of the J. K. Underwood Seed Collection

The J. K. Underwood Seed Collection was largely unorganized and stored in a repurposed map case (Fig. 1a). Individual specimens were stored in old glass vials with deteriorating cork stoppers (Fig. 1b). Each vial had handwritten labels with the specimen's botanical name and 3-part catalog number (Fig. 1c). A random sample of 5.6% of the specimens in the collection (40 of 716) were compared to images from other seed collections and TENN specimens to confirm the reliability of the identifications. Of the 40 specimens examined, only one was found to be misidentified and thus we estimated that the vast majority of the collection (97.5%) is correctly identified. Confirming the identifications of the seeds in the collection and updating determinations as needed is ongoing. To ensure

botanical names were standardized and updated to current accepted names, we used the iPlant Collaborative's Taxonomic Name Resolution Service v4.0 (Boyle et al. 2013, TNRS 2018). The TNRS is a helpful tool for computer-assisted standardization of plant scientific names that corrects alternative spellings or spelling errors to a standard list of names and matches out-of-date names (synonyms) to the currently accepted name.

Our list of 716 specimens with 648 species was entered directly into the "Enter List" tab in TNRS and submitted. Names were validated within the TNRS using the PLANTS (USDA–NRCS 2018), and the Tropicos (Missouri Botanical Garden 2018) databases. Individual specimen names were matched, checked, and updated if necessary within TNRS and returned in a table format. The returned table was then downloaded from the TNRS as a UTF-16 file (.xls). The full exported table was then inspected for errors and incomplete taxonomic information. TNRS failed to return a "best match" for the current accepted botanical name if the specimen names entered were largely incomplete or misspelled. Incomplete or misspelled specimen names from our collection list were individually processed, identified, and updated using the PLANTS (USDA–NRCS 2018) and Tropicos (Missouri Botanical Garden 2018) databases, independent of the TNRS website. Specimens with only a genus name or with specific epithets that could not be read were checked and labeled to the genus level. Once all naming issues were resolved for the full list, a Microsoft Excel file in conjunction with the Mail Merge function in Microsoft Word was used to generate new, updated labels for the collection (Microsoft Office Professional Plus 2010, Version 16.04738.1000, Microsoft Corporation, Redmond, WA).

Labels were printed on acid-free, archival-quality paper and taped inside clear, acid-free polypropylene boxes, into which specimens were transferred (rigid clear hinged plastic boxes, US Box Corporation, Fairfield, New Jersey; Fig. 2a). Box dimensions were $2 \frac{1}{8} \times 1 \frac{5}{8}$ inches (5.38×4.13 cm) for most specimens. Specimens too large to be housed in these boxes (i.e., *Quercus* spp.) were housed in $3 \frac{1}{16} \times 3 \frac{1}{16}$ inches (7.78×7.78 cm) boxes. Specimens were organized alphabetically by genus and specific epithet and placed in inverted lids of herbarium paper boxes, which serve as specimen trays. Dividers were created and inserted into trays to separate specimen boxes, keeping them from shifting when trays are removed (Fig. 2c). Forty boxes of regular dimensions fit into one tray with five columns and eight rows. Trays were labeled alphabetically by genus for the specific collection of specimens per tray (Fig. 2d) and then stored in a metal herbarium cabinet in a temperature and humidity-controlled room at TENN (Fig. 2e). An indexed list with information on each specimen was placed with the collection.

Additions to the Collection

Currently, our seed collection consists only of original specimens collected and deposited at TENN by Dr. Underwood. Our main objective was to update and modernize the collection for use in seed identification. Secondly, enabling the addition of new specimens will help the collection grow in terms of the number of species and the geographical regions they represent, resulting in greater utility of the collection. Optimally, reference collections used for the identification of unknown seeds should contain at least some recent specimens (Nesbitt et al. 2003) because older specimens can often lose morphological details over time, such as coloration, pattern, or texture (Fritz and Nesbitt 2014). Having multiple accessions of the same taxon from different sources has additional advantages. First, any incorrect identifications of reference material are more likely to surface because specimens will not match each other. Second, multiple specimens will better represent the diversity of sizes and shapes potentially present across natural populations (Fritz and Nesbitt 2014). Therefore,



Figure 2. Modern curation of the J. K. Underwood Seed Collection organized alphabetically by genus and then by specific epithet. (a) Specimens are stored in archival-quality clear plastic boxes containing labels with the following information: specific epithet, author, family, and JKU catalog number. (b) The specimens can be easily viewed by eye or under the microscope without removing the seeds from the boxes, decreasing the risk of damage due to physical handling. (c) Boxes are placed alphabetically into cardboard trays with dividers. (d) Trays are labeled alphabetically by genus. (e) Trays are then stored in a fire-proof herbarium cabinet in a temperature- and humidity-controlled room at TENN, which protects the specimens from damage due to insects and/or mold.

enabling new specimens to be added to our collection will result in a better reference tool. Maintaining a dynamic rather than static seed collection will also foster more interactions with the collection by drawing the interest and contributions of contemporary collectors and field botanists.

Our collection is flexible in terms of specimen housing. TENN maintains a large stock of two sizes of plastic boxes (as indicated in our methods above) that are available for additions to the collection. Archival-quality labels for additional specimens will be created according to the scheme laid out in Figure 2, with the difference that new specimens will not have a J. K. Underwood (JKU) catalog number, but instead will list the collector, locality, date, habitat, other relevant collection details, and the collection/catalog number. These physical labels will be taped inside the lids of the specimen boxes. New specimen boxes will be added to trays alphabetically by genus and specific epithet. For trays that are already full (containing 40 small specimen boxes), new trays will be added to the cabinet, specimens shifted, and the tray labels updated to accommodate the additional specimens. New specimens will also be added to the alphabetically indexed list and the hard copy will be updated periodically. Metadata associated with new specimens will be maintained in an Excel spreadsheet available on the plant species pages on our website and backed up on our servers with the future goal to add this data to a relational database as the collection grows.

Donations of seeds associated with zoological studies constitute an exception to the protocol outlined above. TENN was recently gifted a collection of seeds obtained from

mourning dove digestive systems by undergraduate students in a Wildlife, Vegetation, and Habitat course (FWF 325) taught by Dr. Charles Kwit in the Forestry, Wildlife, and Fisheries Department at the University of Tennessee Institute of Agriculture. As part of a class project focused on quantifying bird diets, students used the reference specimens from the J. K. Underwood Seed Collection to identify seeds dissected from the guts and crops of 28 doves from two field sites to family, genus, and occasionally species levels, depending on the quality of the partially digested seeds. After the contents of guts and crops were identified, specimens of each seed species were placed in clear, acid-free polyethylene zip-lock bags, 1.5 × 2 inches (3.81 × 5.08 cm), of 2 mm thickness, containing labels. Bags were then grouped into the larger acid-free polypropylene boxes (7.78 × 7.78 cm) that we used for large specimens in the main seed collection. These large boxes represent individual animals (i.e., Martin 2014). We chose this organizational scheme because this collection will be used for different research purposes than the main J. K. Underwood Seed Collection. Researchers are not likely to use the seeds pulled from animal digestive tracts as a reference for seed identification, because specimens will have undergone mechanical and chemical alteration due to partial digestion. Researchers will likely use this collection either as a comparative collection to examine bird diets, or for collecting data on changes incurred to seeds while passing through a bird digestive system. Thus, grouping seeds by individual animal is our preferred organizational strategy. This zoological seed collection will be stored in a separate cabinet at TENN under environmentally controlled conditions, although we plan to include the family, genus, specific epithet, and metadata associated with these seed specimens in the master Excel spreadsheet as above.

Seed Photography

To enhance the J. K. Underwood Seed Collection and make this resource available to off-site researchers, we photographed representative seeds from the entire collection and will host these images on our website (tenn.bio.utk.edu). Images were taken with a M165 C Leica stereo microscope (Fig. 2b) using one of two lenses: 0.5× PLAN (Leica 10446157) for seeds and fruits larger than 5 mm in diameter, and 1.0× PLANAPO (Leica 10450028) for seeds and fruits smaller than 5 mm, with a total magnification ranging from 8× to 270× (Leica Microsystems, Wetzlar, Germany). Samples were lit with a high diffuse illumination dome that reduces glare and decreases shadows (Leica LED5000). Images 3,500 × 2,600 pixels were generated using z-stacking with 20–30 steps using the Leica MC190 HD camera and the Leica Application Suite X software (2017 Leica Microsystems CMS GmbH 3.3.3.16958) with brightness and contrast automatically adjusted by the software. Large seeded species, such as *Quercus*, were imaged using a Leica MZ6 with a 0.32× (Leica 10422564). A scale bar calculated by the software was included in the images.

Seed morphological diversity was captured in up to four images for each specimen, including a “feature” image of an individual seed (F), typically on a white background to emphasize details on the seed edges (Fig. 3a). Occasionally a black velvet background was used if imaging on the white background resulted in distortions at the edges. A second image highlighting the size, color, or texture variation among multiple seeds (V) was also included for some samples when the seeds from one specimen did not appear identical (Fig. 3b). Typically, a darker cream or brown background was used to emphasize the color and texture variation between seeds. A third image, “fruit and seed” (FS), showed any fruits or inflorescences side by side with a seed if those pieces were included in the specimen (Fig. 3c). The fourth photo presented seeds from two sides, either “dorsal/lateral” (DL), “dorsal/ventral” (DV), or “proximal/distal” (PD) (Fig. 3d). If needed, black modeling clay

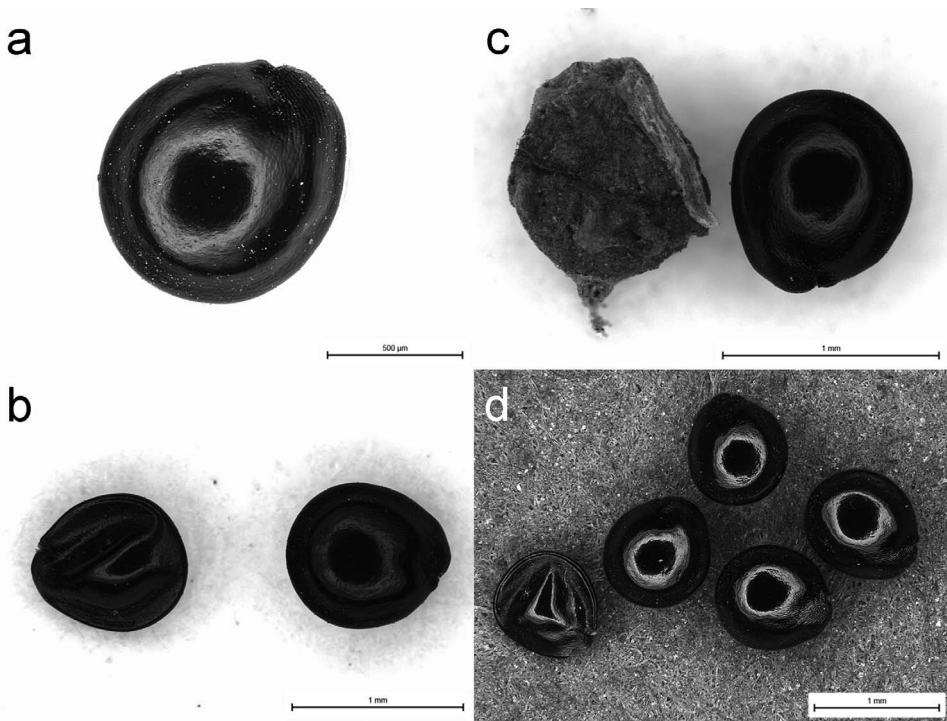


Figure 3. Examples of seed photographs taken and uploaded to the TENN website. (a) Feature (F) photograph. (b) Variation (V) photograph. (c) Fruit and Seed (FS) photograph. (d) Proximal and Distal (PD) photograph. Specimen: *Amaranthus albus* L. Amaranthaceae. JKU #: 56-2-7.

was used to hold the seed in place. No specimens were dissected during the photography process, and if bare seeds were not included in the specimen, whole fruits were imaged in place of seeds. Final images were exported as a JPEG file with the first two letters of the genus, the first four letters of the species epithet, the JKU catalog number, and image type (DL, DV, F, FS, PD, or V) in the file name.

Upload of Seed Photographs to the TENN Website

TENN has an extensive online collection of photos of the native, naturalized, and invasive vascular plants of Tennessee (tenn.bio.utk.edu) that complements our recently published *Guide to the Vascular Plants of Tennessee* (Chester et al. 2015). We are in the process of uploading images of the J. K. Underwood Seed Collection to the TENN website. Uploading these digital images addresses two objectives: (1) to make the collection available to off-site researchers; and (2) to create a digital copy of the collection that preserves the visual attributes of specimens. The TENN website is organized taxonomically, with users selecting species of interest from a series of nested dropdown menus. Users can search by family, genus, or common name; by county; or by state/federal listing. Individual species pages provide photographs of pressed vegetative specimens from the herbarium collection, live plants taken by our staff and donated by friends of TENN, and a Tennessee distribution map highlighting the counties in which the species is known to occur from herbarium specimens at TENN or field observations from botanical experts. For those species represented

THE UNIVERSITY OF TENNESSEE KNOXVILLE

UT Herbarium - TENN



Vascular Plant Herbarium

Database Results

Dicots: **Amaranthaceae**





Species Name: **Amaranthus albus**

Click the thumbnail(s) below to see the enlarged photo.

Amaranthus albus #1 Amaranthus albus #2

Seed Photos


1. 2. am_albu_JKU5627_F 3. am_albu_JKU5627_V 4.

am_albu_JKU5627_PD am_albus_JKU5627_FS

To view a list of all seed specimens housed in the J.K. Underwood Collection at TENN, click [here](#).

Seed Photo Key

First two characters of genus (i.e. xx)
 First four characters of species (i.e. xxxx)
 J.K. Underwood Identification Number (JKU##)
 Seed Image Orientation: PD ("proximal/distal") | DV ("dorsal/ventral") | DL ("dorsal/lateral") | F ("feature") | V ("variation") | FS ("fruit and seed")



Click to see all the species distribution maps or photos under the Genus **Amaranthus**.

NOTE: orange = species presence | grey = species not observed

[Previous Page](#)

If you have any questions or comments, please contact Dr. Jessica M. Budke.

Figure 4. Example of a species page on the TENN website with associated seed photographs from the J. K. Underwood Seed Collection. Seed images are labeled with the following format: xx_xxxx_JKU#_xx, specifying the first two characters of the genus (xx), the first four letters of the species epithet (xxxx), the JKU collection number (JKU#), and image type (xx) in the file name.

in the J. K. Underwood Seed Collection, we are adding associated seed photographs to the species pages, accompanied by a Seed Photo Key describing the information contained in photograph labels (Fig. 4). Users will thus be presented with associated seed photographs when browsing species of interest. Every species page containing seed photographs will also contain a link to an indexed list of the entire J. K. Underwood Seed Collection. Researchers can use this list to determine which species are represented by specimens in the collection, and then look up the images on the website. From there, researchers can decide whether the seed photographs provide sufficient information for their needs, or if physically visiting TENN to see the seeds in person is necessary.

Increasing Visibility of the J. K. Underwood Seed Collection

Uploading photographs of seeds contained in the J. K. Underwood Seed Collection to the TENN species pages will engage users who already visit the website with this reference collection. However, uploading these materials to the website will not increase the collection's visibility beyond the pool of users already familiar with TENN. To more broadly disseminate the availability of this reference collection, we plan on advertising the



Figure 5. Students from Dr. Charles Kwit's FWF 325 class using the J. K. Underwood Seed Collection and other TENN resources for analyzing gut and crop contents of mourning doves.

J. K. Underwood Seed Collection to researchers both on and off campus. As mentioned above, the collection is currently being used in the FWF 325 course. Using the reference specimens, undergraduate students identified seeds dissected from the guts and crops of mourning doves down to family, genus, and occasionally species levels (Fig. 5). This project resulted in an addition to the J. K. Underwood Seed Collection in the form of a zoological seed collection, the curation of which spurred an independent study project at TENN for an undergraduate student in the Forestry, Fisheries, and Wildlife Department. We will continue to encourage Biology instructors to incorporate the seed reference collection and a visit to TENN into their courses, thus exposing undergraduates on campus to the seed collection and herbarium. Additionally, we have integrated the J. K. Underwood Seed Collection into our monthly herbarium event (Specimens and Scones) to which we invite members of the campus community and visiting researchers to tour the herbarium and introduce them to the resources available at our facility.

For nonlocal researchers, we will increase visibility of the seed collection through several mechanisms. TENN is active on social media (Twitter, <https://twitter.com/utkherbarium/>; Instagram, <https://www.instagram.com/utkherbarium/>; and Facebook, <https://www.facebook.com/UTKHerbarium/>) with 798, 263, and 226 followers on each platform respectively as of October 2018, and the followers are continuing to grow. Each month, we plan to highlight one species from our seed collection by attaching a photograph with an accompanying description of the species. Our followers will be reminded of the presence of the collection and may share our posts, thus increasing the collection's visibility. Once the collection has been completely uploaded to our website, we plan to send an email announcing its availability as a community resource to the Herbaria Listserv (<https://www.nacse.org/mailman/listinfo/herbaria>), cosponsored by the American Society of Plant Taxonomists and the Society of Herbarium Curators, which will inform

herbarium researchers and herbarium users beyond our campus. Our objective is to continue to promote the physical and digital use of the J. K. Underwood Seed Collection as a reference collection for seed identification and a repository of seed morphological data for years to come.

DISCUSSION

Working seed reference collections consist of cabinets, drawers, vials, or boxes of identified, labelled seeds and seed-related plant parts, which can be pulled out and compared to unknown specimens (Pearsall 2014). Although the steps we took to curate the J. K. Underwood Seed Collection and integrate specimen photographs into TENN's website were the best choices for our collection, there are many options for curating seed collections and disseminating their visual representations. Modern options for the physical curation of seed collections include a diverse set of storage tools and organizational schemes. For storage of specimens used in genetic and pathogen studies, freezing or cryopreservation are good options. Because most biological activities are greatly minimized under cryogenic conditions (Stanwood and Bass 1981), these methods preserve genetic material, such as RNA for viral and transcriptome research.

For storage of seed collections at room temperature, most systems involve storing seeds in clear plastic or glass containers that allow rapid assessment of seed appearance and restrict the movement of insects that would harm the specimens (Fritz and Nesbitt 2014). A common technique is to store individual accessions from seed collections in glass vials and house these vials in cabinet drawers. According to Nesbitt et al. 2003, this option is advantageous when the amount of seeds per sample is relatively small and the number of accessions large. The Kew Royal Botanic Gardens in London houses their seed collection in this manner. At Kew, 92 vials fit into one drawer of a 30-drawer cabinet, for a total of 2,760 vials per cabinet (Nesbitt et al. 2003). The University of Florida Herbarium (FLAS) also uses vials to store its specimens. FLAS upgraded the housing of its 3,200 seed specimens from old glass vials with cork stoppers and handwritten labels, to modern glass vials with plastic screw-on lids and typed labels that provide easier access to specimens and better protection against insects and fungi. Retaining the use of glass vials 2 1/2 inches (6.35 cm) in length enables FLAS to store the collection in one large and two small antique wooden cabinets (K. Perkins, pers. comm.). Potential disadvantages of this system include the limited number of seeds that can be stored for each accession, although this depends on the size of the vials (typical vials for storing seed samples hold between 0.3 and 0.8 oz [0.3 oz = 8.87 ml and 0.8 oz = 23.66 ml] of volume), and the tendency of tubes to roll around and change position when handled (Nesbitt et al. 2003).

Another technique involves storing samples in plastic boxes. Plastic boxes have the advantage of protecting seeds from degradation by limiting shifting that can be caused by loose vials rolling around and by effectively excluding insects. Each drawer or tray containing specimen boxes can be removed from the cabinet and the seeds easily scanned through the clear boxes, enabling observation of seeds with minimal handling (Nesbitt et al. 2003). The primary disadvantage of this technique is the space required to house a large number of boxed accessions. The Herbarium at the Charles University in Prague (PRC) is home to a recently restored historic seed collection dating from the second half of the 19th century that contains more than 20,000 seed samples from over 13,000 species (Collection of Seeds and Fruits 2018). Beginning in 2009, a student-driven restoration project led PRC to transfer specimens into plastic boxes similar to those we used at TENN to store specimens in the updated J. K. Underwood Seed Collection. Because PRC's modernized collection is now

housed in a new storage cabinet in student offices within the university (Collection of Seeds and Fruits 2018), their curation decisions reflect a design that fosters use of the collection for teaching and forensics purposes.

Curators of seed collections must also make decisions about how to organize specimens. By keeping seed collections separate from vegetative collections, curators have the freedom to make independent choices regarding the use and organization of seed collections, which can be beneficial when collections are targeted for different user groups. Phylogenetic, or taxonomic, systems provide the advantage of grouping closely related taxa together, which is beneficial for identification purposes (Nesbitt et al. 2003). These systems might be preferred by experts who are familiar with the evolutionary relationships among taxa. Traditional taxonomic systems, such as Dalla Torre and Harms (1908), have the benefit of being well-established and thus familiar to a larger body of experts. Modern systems, such as that from the Angiosperm Phylogeny Group (APG 1998, 2003, 2009, 2016), are based on molecular evidence, and the relationships between major lineages have been relatively stable with each updated version (Soltis et al. 2018). Another challenge associated with phylogenetic organizational schemes is that nonexperts can have a more difficult time navigating these collections, rendering them less accessible to students, volunteers, or citizen scientists. Alphabetically-organized collections might be less optimal for research purposes but are preferable when it is desirable to make the collection accessible to nonexperts.

Herbaria today employ both phylogenetic and alphabetical systems to organize seed collections. The J. K. Underwood Seed Collection provides an example of a modernized seed collection that is alphabetically organized. Although at TENN we use a phylogenetic system for organizing our vascular plant collection, we organized our seed collection alphabetically because many of its users are nonexperts, either students or volunteers. FLAS provides an example of an herbarium that employs a taxonomic organizational system for their seed collection. They use a modified version of the Dalla Torre and Harms family numbering system based on the Englerian family delineation and arrangement to organize their seed specimens (Dalla Torre and Harms 1908; FLAS 1995). Although this system is out of date, the Englerian system remains an important cataloging device used by many herbaria around the world, including TENN's vascular plant collections, and enables reasonably easy comparisons of closely related taxa (H. Wilson, 2010, Flowering Plant Taxonomy lecture notes, Texas A&M University). A more modern system for organizing a seed collection taxonomically is based on the recent fourth update of the APG (2016), which is the most up-to-date classification of the orders and families of angiosperms based on contemporary DNA evidence.

Decisions regarding the physical curation are central to seed collection management, because physical collections are the only source for several kinds of biological or anthropogenic data, including aged or ancient seed DNA as well as materials used in germination and viability studies. Physical seed collections are also the cornerstone for reference tools, and it is unlikely that visual representations of any sort can match the quality of physical collections for seed identification and data collection on seed morphology. However, despite the advantages of physically examining specimens, many researchers might be unable to visit remote collections due to the constraints of travel costs. Even in cases where physical collections are visited frequently, they are inherently limited in their range of use, because only one researcher can handle a given specimen at a time. Given these limitations, herbaria are faced with the challenge of not only creating broader access to their seed collections but ensuring that the physical specimens are preserved.

There are many options available for converting physical seed collections into visual representations and for disseminating these images. Creating visual representations of seed specimens can significantly enhance the value of a collection as a reference resource through broader access. Images are easy to distribute to remote researchers and reduce handling of physical specimens. Indeed, visual depictions are generally considered the most effective way of representing seeds, whether through botanical illustrations or high-quality photographs (Herlich and Morell-Hart 2015). Illustrations provide technical detail and have traditionally been preferred over photographs because they can capture the three-dimensionality of seeds (Herlich and Morell-Hart 2015). However, illustrations take significant amounts of time to generate, and require an artist with the expertise. Photographs are easier to create and typically do not require a highly skilled technician to produce. As with botanical illustrations, photographs provide information on the general morphology, size, color, texture, and form of seeds. Additionally, with advances in technology, such as z-stacking, photographs are now also able to capture the three-dimensional nature of seeds. Thus, digitizing and disseminating seed collections through photography can expand their use beyond that of physical collections.

There are many strategies for photographing seeds. Through the efforts of the Seed Herbarium Image Project (SHIP) in 2004, Harvard University's Seed Herbarium at the Arnold Arboretum employed high resolution digital photography to visually document the seed morphology of their collection (Seed Herbarium 2018). Containing more than 2,100 specimens dating from the 1960s to the present, the Seed Herbarium's digital database contains multiple images for each specimen, including seeds and seed-associated plant parts arranged to showcase different aspects of morphology and phenotypic variation. The Seed Herbarium's images were all taken on a matte gray background, which provides a neutral and nondistracting base for viewing specimens. Images also include a ruler under the specimen for measurements. Many images include a perpendicular set of delineation lines next to the specimen, containing an abbreviation signifying the plant part the photograph is depicting. A key for abbreviations is included on the SHIP webpage. The upper corner of each photograph contains a list of information about the image, including species name, the dimensions (length and width) of each plant part, and the accession number associated with the imaged specimen (Seed Herbarium 2018).

The Seed ID Workshop (OARDC Seed ID Workshop 2018) at the Department of Horticulture and Crop Science at Ohio State University employs a slightly different photographic strategy for their seed collection. Images were taken on a bright green background that starkly contrasts the specimens. This provides the advantage of clearly delineating seed outlines and textures, although the bright color might be distracting in some cases. Most images include a ruler to the left of the specimen for measurements, and some images contain multiple seed and plant parts. Other specimens are represented by multiple separate images of seed and plant parts to highlight phenotypic variation. Decisions regarding the number of plant parts to include in a single photograph versus multiple photographs appear to have been made based on the size of specimens and the diversity of morphological or phenotypic forms. Each photograph in the Seed ID Workshop has the specimen's family listed at the top of the image, and the species name at the bottom (OARDC Seed ID Workshop 2018).

The Seed Information Database (SID; Kew Royal Botanic Gardens 2018) in London provides yet another example of the variability of seed photographic techniques. SID contains multiple images of different seed-affiliated plant parts, each identified by a filename describing the type of image taken. Filenames include genus, species, the sequential num-

ber for images taken for a single taxon, and an acronym representing the plant part shown (i.e., “D” for diaspore). Image types include fruits, diaspores, the mechanical protection of the seed, and seeds. All images were taken on matte white backgrounds, which focuses the user’s attention on seed detail, and often major seed parts are labeled (e.g., cotyledon, seed coat). Images also contain scale bars for measurements. Scale bars are typically in the lower right-hand corner or upper left-hand corner of the image and cover roughly 30% of the image space represented by the specimen (Kew Royal Botanic Gardens 2018).

Digital seed collections are often organized and accessible in various ways, thus enabling researchers to search for images based on different characteristics. Harvard University’s Seed Herbarium database of images is searchable through scientific name, family, or Arboretum accession number. This method of organizing seed images online provides the advantage of enabling users to directly search for their taxon or specimen of interest. In addition to the specimen images, the Seed Herbarium website provides useful information about each image, including the species name, family, accession number, geographic location where the specimen was collected (including GPS coordinates when available), the Harvard University Herbarium barcode associated with the specimen, and the photo credit and copyright information for each image (Seed Herbarium 2018). The OARDC Seed ID Workshop (2018) database seed images hosted on their university website are similarly organized through searchable lists alphabetized by scientific name, common name, or family. This method of organizing seed images has advantages and disadvantages that echo those associated with organizing a physical seed collection alphabetically, although a digital repository of images has the added advantage that it can be searched and accessed in multiple ways. Accompanying seed images on each species page is a searchable bulleted list of all of the other specimens represented in the family (OARDC Seed ID Workshop 2018). SID is a flexible platform that can be searched by seed taxonomy, storage behavior, weight, dispersal form, germination, oil and protein content, salt tolerance, or morphology (Kew Royal Botanic Gardens 2018). These search options provide users with an advanced set of tools for sifting through online seed data, which enables specimens to be accessed in several unique ways, thus serving a greater diversity of research projects. Many institutions employ diverse and effective techniques for seed collection management, and our discussion of curation options is not exhaustive. However, the examples above summarize many of the common techniques for curating and digitizing seed collections and provide a decision-making framework for the management of such collections.

Although distinct, these curation and digitization efforts are unified in their objectives to not only modernize and increase the visibility and use of seed collections, but to participate in the broad dissemination of botanical information. Beyond technical elements, visualization of these reference materials is best realized through successful partnerships across sub-disciplines, where interdisciplinary collaboration, as well as work with an extended network of experts, enhances the base of knowledge to which we all have access (Herlich and Morell-Hart 2015). Widely disseminating digital representations of seed collections thus not only increases awareness of such reference tools, benefitting the associated organization, university, or herbarium by extension, but enhances the research community as a whole by encouraging cross-disciplinary communication, sharing of ideas, and collaboration.

CONCLUSIONS

The process of rediscovering the J. K. Underwood Seed Collection, modernizing its curation, photographing its specimens, and advertising its utility as a seed identification reference collection was a rich learning experience for TENN students and staff.

Historic collections, even those that are poorly curated, potentially damaged, missing associated metadata, or with out-of-date scientific nomenclature, remain a source of untapped research potential. The initial building of a reference collection includes the associated field work and time spent identifying the samples, which can be very labor- and time-intensive. Bringing historic collections back into the light thus preserves the work of past collectors and curators. Historic collections can add value to existing collections and can form the foundation for new and expanding collections. Although physical collections might be the primary focus of curation efforts, they alone can be limited in terms of accessibility. Creating and disseminating images of seed collections fosters cross-disciplinary communication and collaboration, which is critical to the future of many disciplines that rely on such information. This case study illustrates some of the options available to herbarium staff when faced with the curation challenges of a historic seed collection. We enthusiastically encourage curators to increase the visibility of their historic seed collections through additional curation, imaging, and online availability.

ACKNOWLEDGMENTS

The authors thank B. Eugene Wofford for saving these specimens from being discarded for years, despite pressure to throw them away. We appreciate the insightful comments provided by Barbara M. Thiers that helped to improve this manuscript. We would also like to thank Kent D. Perkins with the University of Florida Herbarium for information on the curation of FLAS's seed collection. The L. R. Hesler Endowment generously funded graduate research assistantships to CNM and IMW and supplies for this project.

LITERATURE CITED

- [APG] Angiosperm Phylogeny Group. 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85:531–553.
- APG. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141(4):399–436.
- APG. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161(2):105–121.
- APG. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181:1–20.
- Bebber, D.P., M.A. Carine, J.R. Wood, A.H. Wortley, D.J. Harris, G.T. Prance, G. Davidse, J. Paige, T.D. Pennington, N.K.B. Robson, and R.W. Scotland. 2010. Herbaria are a major frontier for species discovery. *Proceedings of the National Academy of Sciences U S A* 107(51):22169–22171.
- Besnard, G., P.A. Christin, P.J.G. Malé, E. Lhuillier, C. Lauzeral, E. Coissac, and M.S. Vorontsova. 2014. From museums to genomics: Old herbarium specimens shed light on a C₃ to C₄ transition. *Journal of Experimental Botany* 65(22):6711–6721.
- Bhattacharai, K.R., O.R. Vetaas, and J.A. Grytnes. 2004. Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography* 31(3):389–400.
- Bolmgren, K. and K. Lönnberg. 2005. Herbarium data reveal an association between fleshy fruit type and earlier flowering time. *International Journal of Plant Sciences* 166(4):663–670.
- Boyle, B., N. Hopkins, Z. Lu, J.A.R. Garay, D. Mozzherin, T. Rees, N. Matasci, M.L. Narro, W.H. Piel, S.J. McKay, S. Lowry, C. Freeland, R.K. Peet, and B. Enquist. 2013. The taxonomic name resolution service: An online tool for automated standardization of plant names. *BMC Bioinformatics* 14:16. doi:10.1186/1471-2105-14-16.
- Bridge, R.R. and W.R. Meredith. 1983. Comparative performance of obsolete and cCurrent cotton cultivars 1. *Crop Science* 23(5):949–952.
- Chester, E.W., S.E. Wofford, J. Shaw, D. Estes, and D.H. Webb. 2015. *Guide to the Vascular Plants of Tennessee*, 1st ed. The University of Tennessee Press, Knoxville.
- Chown, S.L., A.H. Huiskes, N.J. Gremmen, J.E. Lee, A. Terauds, K. Crosbie, Y. Frenot, K.A. Hughes, S. Imura, K. Kiefer, M. Lebouvier, B. Raymond, M. Tsujimoto, C. Ware, B. Van de Vijver, and D.M. Bergstrom. 2012. Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Sciences U S A* 109(13):4938–4943.

- [CNABH] Consortium of North American Bryophyte Herbaria. 2018. <http://bryophyteportal.org/portal/index.php> (21 March 2018).
- Collection of Seeds and Fruits. 2018. *Herbarium Collections at the Charles University in Prague (PRC)*. <https://botany.natur.cuni.cz/cevnate/prc/seedfruit.php> (5 March 2018).
- Dalla Torre, C.G. and H. Harms. 1908. *Register zu de Dalla Torre et Harms: Genera Siphonogamarum ad Systema Englerianum Conscripta*. W. Engelmann, Leipzig [Germany]. Facsimile reprint by Verlag von H. R. Engelmann (J. Cramer), Weinheim [Germany]. 1958. 568 pp.
- Elith, J. and J. Leathwick. 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions* 13(3):265–275.
- [FLAS] University of Florida Herbarium. 1995. *Protocols for Working with the Seed Collection*. Florida Museum of Natural History. <https://www.floridamuseum.ufl.edu/herbarium/policy/seedcollectionprotocols.htm> (5 March 2018).
- Fritz, G. and M. Nesbitt. 2014. Laboratory analysis and identification of plant macroremains. Pp. 115–145 in *Method and Theory in Paleoethnobotany* (J.M. Marston, J.D' Alpoim Guedes, and C. Warinner, eds.). University Press of Colorado, Boulder. 548 pp.
- Herlich, J.M. and S. Morell-Hart. 2015. Visualization and collaborative practice in paleoethnobotany. *SAA Archaeological Record* 24–32.
- Higgins DeSmet, N. 2017. *Scientists laud firefighters' care of UVM plant collection*. Burlington Free Press, USA Today. <https://www.burlingtonfreepress.com/story/news/local/vermont/2017/08/07/burlington-fire-dept-praised-quick-work-uvm/545283001/> (17 April 2018).
- Holland, J.M., M.A.S. Hutchison, B. Smith, and N.J. Aebischer. 2006. A review of invertebrates and seed-bearing plants as food for farmland birds in Europe. *Annals of Applied Biology* 148(1):49–71.
- [iDigBio] Integrated Digitized Biocollections. 2018. The National Resource for Advancing Digitization of Biodiversity Collections, the National Science Foundation. <https://www.idigbio.org/about-idigbio> (21 March 2018).
- James, S.A., P.S. Soltis, L. Belbin, A.D. Chapman, G. Nelson, D.L. Paul, and M. Collins. 2018. Herbarium data: Global biodiversity and societal botanical needs for novel research. *Applications in Plant Sciences* 6. e01024. DOI: 10.1002/aps3.1024.
- Kew Royal Botanic Gardens Seed Information Database (SID). 2018. <http://data.kew.org/sid/> (5 March 2018).
- Kitamura, S., S. Suzuki, T. Yumoto, P. Chuailua, K. Plongmai, P. Poonswad, N. Noma, T. Maruhashi, and C. Suckasam. 2005. A botanical inventory of a tropical seasonal forest in Khao Yai National Park, Thailand: Implications for fruit–frugivore interactions. *Biodiversity and Conservation* 14(5):1241–1261.
- Leino, M.W., J. Hagenblad, J. Edqvist, and E.M.K. Strese. 2009. DNA preservation and utility of a historic seed collection. *Seed Science Research* 19(3):125–135.
- Loiselle, B.A., P.M. Jørgensen, T. Consiglio, I. Jiménez, J.G. Blake, L.G. Lohmann, and O.M. Montiel. 2008. Predicting species distributions from herbarium collections: Does climate bias in collection sampling influence model outcomes? *Journal of Biogeography* 35(1):105–116.
- Martin, T. 2014. Curating ethnozoological and zooarchaeological collections. Pp. 85–96 in *Curating Biocultural Collections, A Handbook* (J. Salick, K. Konchar, and M. Nesbitt, eds.). Royal Botanic Gardens, Kew, Richmond, Surrey, UK. 406 pp.
- Millennium Seed Bank. 2018. Kew Royal Botanic Gardens. <https://www.kew.org/wakehurst/attractions/millennium-seed-bank> (17 October 2018).
- Missouri Botanical Garden. 2018. *Tropicos*. St. Louis. <http://www.tropicos.org> (20 March 2017).
- National Park Service. 2018. Great Smoky Mountains. <https://www.nps.gov/grsm/learn/nature/plants.htm> (28 March 2018).
- Nesbitt, M., S. Colledge, and M.A. Murray. 2003. Organisation and management of seed reference collections. *Environmental Archaeology* 8:77–84.
- [OARDC] Ohio Agricultural Research and Development Center Seed ID Workshop. 2018. OARDC, The Ohio State University. <https://www.oardc.ohio-state.edu/seedid/search.asp> (5 March 2018).
- Ortiz-García, S., E. Ezcurra, B. Schoel, F. Acevedo, J. Soberón, and A.A. Snow. 2005. Absence of detectable transgenes in local landraces of maize in Oaxaca, Mexico (2003–2004). *Proceedings of the National Academy of Sciences U S A* 102(35):12338–12343.
- Parzies, H.K., W. Spoor, and R.A. Ennos. 2000. Genetic diversity of barley landrace accessions (*Hordeum vulgare* ssp. *vulgare*) conserved for different lengths of time in *ex situ* gene banks. *Heredity* 84(4):476–486.
- Pearsall, D.M. 2014. Curating palaeoethnobotanical specimens and botanical reference collections. Pp. 67–83 in *Curating Biocultural Collections, A Handbook* (J. Salick, K. Konchar, and M. Nesbitt, eds.). Royal Botanic Gardens, Kew, Richmond, Surrey, UK. 406 pp.

- Santos, E.F., E.Z. Setz, and N. Gobbi. 2003. Diet of the maned wolf (*Chrysocyon brachyurus*) and its role in seed dispersal on a cattle ranch in Brazil. *Journal of Zoology* 260(2):203–208.
- Savolainen, V., P. Cuénot, R. Spichiger, M.D. Martinez, M. Crèvecoeur, and J.F. Manen. 1995. The use of herbarium specimens in DNA phylogenetics: Evaluation and improvement. *Plant Systematics and Evolution* 197(1–4):87–98.
- Schatz, G.E. 2002. Taxonomy and herbaria in service of plant conservation: Lessons from Madagascar's endemic families. *Annals of the Missouri Botanical Garden* 89(2):145–152.
- Seed Herbarium. 2018. The Arnold Arboretum of Harvard University. <https://www.arboretum.harvard.edu/plants/herbaria/seed-herbarium/>(5 March 2018).
- [SERNEC] Southeast Regional Network of Expertise and Collections. 2018. Appalachian State University, Boone, North Carolina. <http://serneportal.org/portal/> (21 March 2018).
- Smith, H.C. 1999. *An Honored Calling: A History of the College of Agricultural Sciences and Natural Resources*. (L.B. Gary, ed.) Institute of Agriculture, University of Tennessee, Knoxville. 94 pp.
- Soltis, D., P. Soltis, P. Endress, M. Chase, S. Manchester, W. Judd, L. Majure, and E. Mavrodiev. 2018. *Phylogeny and Evolution of the Angiosperms*, Revised and updated ed. University of Chicago Press, Chicago, Illinois. 580 pp.
- Staats, M., R.H. Erkens, B. van de Vossen, J.J. Wieringa, K. Kraaijeveld, B. Stielow, J. Geml, J.E. Richardson, and F.T. Bakker. 2013. Genomic treasure troves: Complete genome sequencing of herbarium and insect museum specimens. *PLoS One* 8(7), E69189.
- Stanwood P.C., and L.N. Bass. 1981. Seed germplasm preservation using liquid nitrogen. *Seed Science and Technology* 9:423–437.
- Svalbard Global Seed Vault. 2018. *Crop Trust*. <https://www.croptrust.org/our-work/svalbard-global-seed-vault/> (17 October 2018).
- Thiers, B. 2018. The world's herbaria 2017: A summary report based on data from Index Herbariorum. *Index Herbariorum* 2(1):1–19.
- [TNRS] Taxonomic Name Resolution Service. 2018. *iPlant Collaborative*. Version 4.0 <http://tnrs.iplantcollaborative.org> (20 March 2017).
- Underwood, J.K. 1955. *Planting and Care of Tennessee Lawns*. Agricultural Extension Service, University of Tennessee, Knoxville. 28 pp.
- Underwood, J.K. 1973. *Establishment, Care and Maintenance of Tennessee Lawns*, Revised ed. Agricultural Extension Service, The University of Tennessee, Knoxville. 47 pp.
- [USDA–NRCs] US Department of Agriculture–National Resources Conservation Service. 2018. *PLANTS Database*. National Plant Data Team, Greensboro, North Carolina. <http://plants.usda.gov> (20 March 2017).
- Wadley, L. 2004. Vegetation changes between 61,500 and 26,000 years ago: The evidence from seeds in Sibudu Cave, KwaZulu-Natal. *South African Journal of Science* 100(3–4):167–173.
- Walker, C.L. 2016. *Retiree Biographies*. University of Tennessee Institute of Agriculture. Department of Plant Sciences. <https://ag.tennessee.edu/plantsciences/Documents/RetireeBiographies/JudsonUnderwoodBio.pdf> (6 March 2018).
- White, P.S. 1981. Looking for *Linnaea*: The high Smokies still protect some secrets on their rugged slopes. *Tennessee Conservationist* 48(5):14–16.
- Wolf, J.H., and F.S. Alejandro. 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography* 30(11):1689–1707.