North American Herbaria and their Tropical Plant Collections: What exists, what is available, and what the future may bring

Vicki Ann Funk

SCI.DAN.B. 6 · TROPICAL PLANT COLLECTIONS
THE ROYAL DANISH ACADEMY OF SCIENCES AND LETTERS · 2017

Abstract

Herbaria, and biological collections in general, provide an invaluable record of the diversity of plants and animals through time and space and are used in studies addressing climate change, tracking invasive species, niche modeling, and assembling the tree of life. They are our only direct documentation of biological diversity and therefore serve as essential tools for research and education in biological sciences. According to Index Herbariorum there are ~2885 registered herbaria containing approximately 375,480,850 specimens. In North America there are 723 herbaria and over 85 million specimens accounting for 25% of the herbaria and 23% of the collections in the world. Herbaria in North America began by exploring local plant diversity, and over time some became research centers with broader interests. In fact, the 33 largest herbaria in North America (those with at least 600,000 collections) hold 63% of the specimens and have substantial holdings from outside the area. Nearly all of these large institutions were founded in the mid 1800's (oldest is the collection of the Academy of Natural Sciences, Philadelphia in 1812) and have large collections from the Neotropics. An informal investigation indicated that non-North American collections account for about half of those housed in the larger North American institutions. The 20th Century was a period of expansion and a large number flora and inventory projects were started, so it was characterized by intensive collecting, and staff growth fuelled by these projects. However, by the late 20th Century the creation of these projects had slowed as funding for such baseline efforts had mostly disappeared in North America to be replaced by question driven research that sponsors more targeted collecting efforts. Today many herbaria are under-valued, and their existence is threatened. More small and medium sized herbaria, especially at universities, are being downsized or closed and some are relocated to larger herbaria, removing them from their niche and creating additional pressure on the budgets of their new home. In the early days, collecting expeditions took most material to their home institutions. However, in the last 30 years, most large herbaria have increased their collaboration with tropical institutions by providing access to valuable historical collections and literature as well as graduate education and training allowing them to further develop their research and collecting programs. As a result, multinational projects are now underway leading to the discovery and documentation of tropical plant diversity and a shared responsibility for both the collection and preservation of specimens. Today staff and students from tropical herbaria are leading the majority of the collecting trips and sponsoring most new floras and inventory projects in the tropics. North American herbaria and their counter parts in the tropics are colleagues as well as friends, and are working together to document biodiversity and provide stability for collections everywhere.

Key Words: biological collections, foundation of new herbaria, growth of herbaria, relationships between temperate and tropical herbaria

Vicki Ann Funk, US National Herbarium, Department of Botany, NMNH-MRC166, Smithsonian Institution, Washington DC, 20013-7012 USA. E-mail: funkv@si.edu

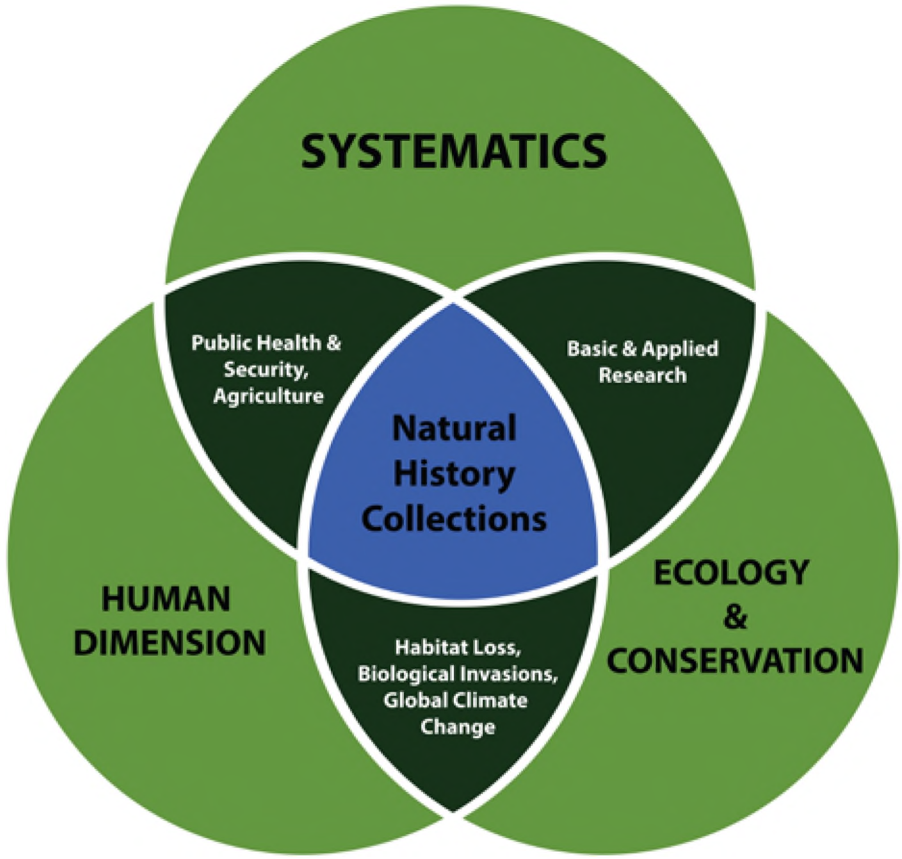
Biological collections provide an invaluable record of the distribution of biodiversity throughout the world and through recent and geological times, and they are the only direct documentation of the biological, physical, and cultural diversity of the planet (Wen *et al.* 2015).

There is an essential link between the economy and the environment, and we must recognize that the health of our lands, waters, plants, and animals is essential to our survival. To protect these resources we need a continuously expanding knowledge base to formulate environmental and economic strategies. Biodiversity collections are the foundation of this knowledge base.

Natural history museums, botanical gardens, universities, and other repositories of biological collections house an enormous number of specimens of organisms from around the world and through time. The total number is estimated to be 3 billion (Kemp 2015), but data from this study indicate that it may be closer to 5 billion (see discussion below). These traditional samples are accompanied by countless ancillary collections found in associated libraries and archives housing illustrations, microscope slides, seed and wood samples, databases, photographs, films, and more. All collections contain data about a specific point in time and space, and the collective information of all of these data is enormous. Such data syntheses are used to study change through time by organisms, earth, our solar system and the Universe. From basic questions such as: "How many species are there?", "How do we tell them apart?", "Where do they grow/live?", "How are they related to one another?" and "How should we classify them?" to using these data as the foundation for our investigations into the evolutionary and biogeographic history of the organisms we study as well as to estimate and document global patters of biodiversity, predict the effects of climate change on diversity, determine what areas should be conserved, and a host of other evolution and conservation related questions (Fig. 1).

There have been many articles that address the importance of collections (e.g. Funk 2003a, 2003b, 2006; Holmes *et al.* 2016; Kemp 2015; SA2000 1994; Wen 2015), and there are also many recent examples of the use of plant collections for a variety of topics including work on the 'origin of temperate forests' (Manos & Meireles 2015) and studies, based on specimen information, that document and predict climate change (Ellis *et al.* 2012; Johnson *et al.* 2011; Primack *et al.* 2004). Likewise collections have been used for studies on species loss and the increase and decrease in total species based on the timing of the introduction of invasive species (Ellis *et al.* 2012; Feeley 2012; Martin *et al.* 2014), and collections data have been combined with microsatellite data and habitat modelling to test competing hypotheses concerning historical distributions (Fant *et al.* 2014). One of the most frequent uses is as a repository for vouchers from surveys, chromosome and pollen studies, molecular sequencing, etc. These are extremely important, given that the identifications on herbarium material may need to be verified. For instance, Goodwin *et al.* (2015) have shown that of the 4500 specimens of African gingers that

Fig. 1. The importance of natural history collections in science and society (with permission from Wen *et al.* 2015)



they studied, 58% were misidentified, and 29% of the Dipterocarps had different names on the same collection housed in different herbaria. Without vouchers, we cannot know with certainty, the name that goes with the sequence, the pollen grain image, or the chromosome number. Of course, an additional importance of collections is that they are mined for leaf material for DNA-based studies, and this is likely to increase as next generation sequencing increases the usability of fragmented DNA, for instance, Beck and Semple (2015) used Next-generation sampling pairing genomics with herbarium specimens to give a species-level signal in *Solidago* (Compositae) and 93 of the 95 herbarium specimens (5-45 years old) were sequenced successfully using an Illumina platform. These examples are few, but they show that biodiversity collections, and herbaria in particular, are not static repositories, instead they are windows into the past, present, and future and essential tools for research in biological sciences (Fig. 2; Funk 2003a, 2003b; Johnson 2015; Schilthuizen *et al.* 2015).

Here the focus is on herbaria, where scientists and natural historians have documented earth's plant and fungal diversity for over 300 years through specimen preservation and study. From the time of Linnaeus, explorers traveled the globe bringing back preserved and living plant material to be studied and grown, first in Europe and then North America. Some countries did a good job of setting up local herbaria and gardens that ultimately provided a sound foundation for biodiversity studies in those countries, others did not.

The first documented herbaria were in Europe, and it was not until the mid-1800's that North American herbaria came into prominence. Keeping in mind the importance of collections and how central they

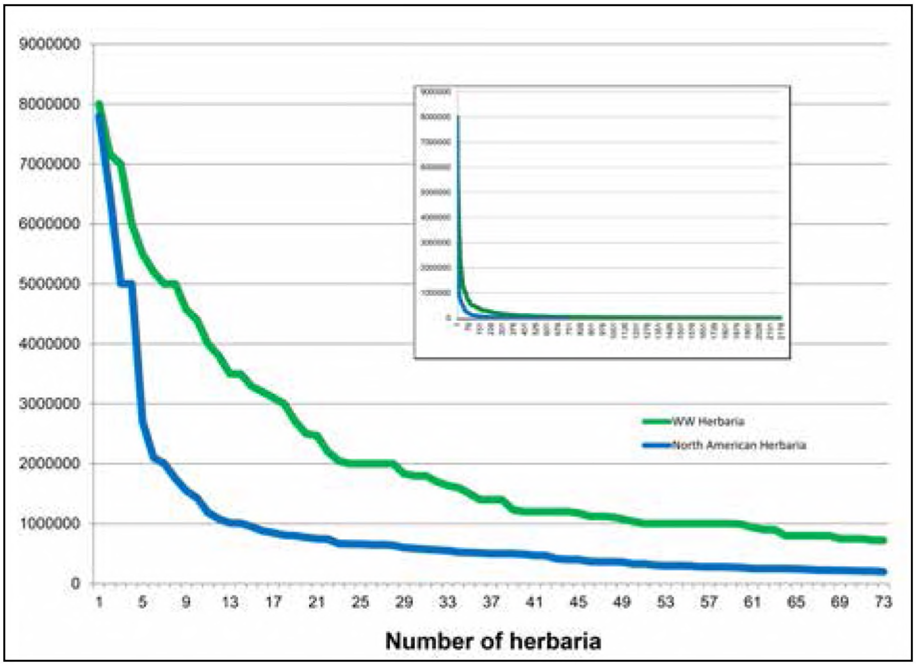


Fig. 2. Number of specimens (Y axis) in the 73 largest herbaria (larger graph) and number of specimens in all herbaria (smaller graph). Both North American herbaria and herbaria world wide ('WW Herbaria') are shown.

are to scientific and conservation studies and to questions concerning endangered species, climate change, and invasives, etc., we can examine where the tropical collections are located in North American (north of Mexico) and discuss their accessibility.

Materials and Methods

The primary source of information for this study was a version of *Index Herbariorum* that was downloaded in March 2016 as a csv file and converted into Excel (IH; Thiers continuously updated). Several entries that appeared to be in need of new information were updated by contacting the person in charge of the herbarium or by accessing the herbarium's website. All numbers used in this study should be considered approximate, as there is always some confusion as to what collections are reported for each herbarium Code (abbreviation).

Index Herbariorum (IH) is a guide to the herbaria of the world. Participation is free and voluntary but the benefits are so great that most herbaria of any size join. The IH entry for each herbarium includes its mailing address, URL, a description of its contents (e.g. number and type of specimens), founding date, as well as names, contact information and areas of expertise of associated researchers. Each institution is assigned a permanent unique identifier in the form of a one to eight letter code (sometimes called an abbreviation or incorrectly an acronym), a practice that dates from the founding of IH in 1935. These codes were used throughout this study and a list of all herbaria cited in this paper can be found in the Appendix. The 'International Association for Plant Taxonomy' (IAPT; then housed at U) published the first six editions of IH (1952-1974). Patricia Holmgren, then director of the New York Botanical Garden Herbarium (NY), was senior editor of the subsequent two editions, ed. 7-8. The last hard copy of IH was ed. 8, published in 1990 (Holmgren *et al.* 1990), and since then the index has been available only online. In September 2008, Barbara M. Thiers, Director of the NY Herbarium (now Vice President for Science) became the editor (Thiers, continuously updated). Soon the website will allow users to update their own records, which should allow faster updates and less work by NY staff. For the purpose of this study, a few changes were made in the data from IH the most important one was that herbaria that are located at the same physical address but with different codes were combined (e.g., CAN* = CAN + CANA + CANL + CANM). The goal was to obtain a clear idea of the amount of resources available at a single facility and to determine the origin of the material. This kind of change was only done a few times and they are clearly indicated in the Appendix.

It is important to remember that all information in IH is 'self-reported' and therefore relies on the accuracy of the numbers provided by the individual herbaria. Some herbaria such as CANB and P have a good idea of how many specimens they have, while others are forced to use a metric (i.e. number of cases times the estimated average number of sheets per case) to obtain an estimated number. More and more herbaria are attempting to obtain accurate numbers, and so results of future studies should be more precise.

Results and Discussion

There are 2885 herbaria listed in IH (that have useful information) housing 375,480,850 specimens (Table 1). However, a large percentage of the specimens (36%; 137,350,297; Tables 1 & 2) are found in the 34 largest herbaria (those with 2,000,000 or more specimens; Tables 1 & 2). In North America there are 723 herbaria with 85,530,469 specimens (23% of WW total). North American herbaria with 550,000 or more specimens (top 33; Table 3) provide 63% of the specimens found in North America. In fact the four largest herbaria in North America have more than 24,400,000 specimens which is more than 28% of the total holdings in North American herbaria.

We can use these data to estimate the total number of collections in museums and academic institutions worldwide. We know, based on figures in IH, that there are 76,187,380 herbarium specimens in the USA and we know the global total (375,480,850) so approximately 20% of the World's herbarium specimens are located in the USA. Taking that one step farther, it has been estimated that we have 1 billion collections (of all organisms) in the USA (Kemp 2015), if that also represents 20% of the global collections then we must have closer to 5 billion specimens globally rather than the 3 billion mentioned by Kemp (2015).

Table 2 presents a worldwide listing of herbaria based on the number of collections they hold and provides information on the geographic location(s) where most of the collections were gathered. The list is broken into seven groups each of which is separated by a natural gap in the number of specimens. Four of the top 12 herbaria (by number of specimens; Table 2) are located in North America, with NY ranking as the

Table 1. Number of herbaria world-wide (WW) and in North America (NoAm; north of Mexico). **Blue Bold** indicate North American herbaria.

Number of herbaria world wide	**2,885**	
Number of specimens (total)		**375,480,850**
Number of specimens in the **34** largest herbaria	**137,350,297** [36%]; all herbaria	≥2,000,000

Number of herbaria in North America	**723 [25% of WW]**	**(Canada 84 + USA 639)**
Number of specimens (total)	**85,530,469 [23% of WW]**	
Number of specimens in **33** largest herbaria	**53,553,400 [63% of NoAm]**	≥550,000

Table 2. The largest herbaria in the World and the origin of their specimens. See appendix for city and country of each herbarium code. Groups were determined by natural breaks in collections size. If two herbaria have the same number of specimens, they are ordered by herbarium code. When two or more herbaria with a different herbarium code have the same physical address they are combined and are indicated in the tables with an * and listed in the Appendix. WW stands for collections with world wide coverage. **Bold blue** indicates North American Herbaria, **Bold red** indicates tropical herbaria, **Bold green** indicates Asian and Pacific non-tropical herbaria, Black indicates herbaria in the rest of world, mainly in Europe, Eurasia, and the UK.

Rank	Code (in *Index Herbariorum*)	Number of specimens	Strength
Group 1			
1	P*	8,000,000	WW, especially Africa, Madagascar, SE Asia, New Caledonia, former French Territories.
2	**NY**	**7,800,000**	**WW, especially USA, tropical Americas.**
3	LE	7,160,000	WW, especially temperate.
4	K	7,000,000	WW, especially Africa, Asia, Brazil, Australasia.
Group 2			
5	**MO**	**6,500,000**	**WW, especially tropical Americas, Africa, Madagascar.**
6	G	6,000,000	WW, especially Mediterranean, Middle East, South America, Africa, Madagascar.
7	L	6,000,000	WW, especially tropical Asia, tropical Africa, Pacific, Europe, Central & South America.
Group 3			
8	W	5,500,000	WW.
9	BM	5,200,000	WW, especially Africa, North America, West Indies, Himalaya.
10	**US**	**5,100,000**	**WW, especially the Americas, Pacific Islands, Philippines, India.**
11	**GH**	**5,005,000**	**WW, temperate Areas, West Indies, Mexico, Asia, Malaysia.**
12	FI	5,000,000	WW, especially Mediterranean.

Group 4

13	S	4,570,000	WW.
14	LY	4,400,000	WW.
15	BR	4,000,000	WW, especially Belgium, Central Africa.

Group 5

16	B	3,800,000	WW, especially Europe, Mediterranean, SW Asia, Africa, South America.
17	JE	3,500,000	WW, especially Europe, SW Asia, Cuba.
18	MPU	3,500,000	WW, especially Mediterranean, Africa, Americas.
19	H	3,290,500	WW, especially areas of boreal and temperate Northern Hemisphere.
20	M	3,200,000	WW.
21	UPS	3,100,000	WW.
22	E	3,000,000	Especially Asia, Arabia, Turkey, Bhutan, Brazil, Mediterranean, Chile, Argentina, S Africa.

Group 6

23	C	2,707,000	WW, especially Nordic countries, Greece, Ethiopia, Thailand, South America.
24	F	2,700,000	WW, especially tropical and North America.
25	LD	2,500,000	WW especially Scandinavia, Mediterranean, South Africa.
26	PE	2,469,596	WW, especially China.

Group 7

27	PRC	2,200,000	WW, especially central Europe, Carpathian Mts., Balkan Peninsula.
28	UC	2,100,000	WW, especially California, w. North Am., Mexico, Andes, Pacific, E Asia.
29	KW	2,048,200	WW, especially Ukraine.
30	BO	2,000,000	Flora Malesiana region.
31	CAL	2,000,000	Especially India, S & SE Asia.
32	CAS	2,000,000	WW, especially W North America, N Latin America, Europe, China, Galapagos.
33	PR	2,000,000	WW, especially Czech Rep., Slovakia, Europe, Balkan Peninsula, Australia, Iraq, Iran.
34	ZT	2,000,000	WW.

End of consecutive numbers - Miscellaneous Group

39	TI	1,700,000	Vascular Plants of E & SE Asia.
40	TNS	1,636,000	WW, vascular plants, mainly of Japan.
42	DAO*	1,550,000	Especially Canada, north temperate plants.
47	MEXU	1,400,000	New World, especially Mexico, Central America.
50	MEL	1,200,000	WW, Australia, especially Victoria.
51	NSW	1,200,000	WW, Australia, especially New South Wales.
52	PRE	1,200,000	Southern Africa, some from other parts of Africa.
57	KUN	1,114,000	China, especially Yunnan, Sichuan, Guizhou, Tibet; SE Asia.
59	ENCB	1,080,000	Mexico and neighboring areas.
61	AD	1,040,000	WW, especially Australia.
62	CAN*	1,010,500	North Temperate regions, especially Canada.
66	EA	1,000,000	Especially E Africa and other African countries.
67	IBSC	1,000,000	China, especially tropical and subtropical parts.

Table 3. North American Herbaria with more than 550,000 specimens and the origin of their collections. Herbaria that are combined are indicated with an *.

Rank	Code (in Index Herbariorum)	Number of specimens and their origin, strength
Group 1		
1	NY	7,800,000 (50% tropical; most from Americas)
2	MO	6,500,000 (70% tropical; Americas, Africa, Asia)
Group 2		
3	US	5,100,000 (60% tropical; most Americas, Pacific)
4	GH	5,005,000 (25% tropical; World Wide, strong in North America and Europe, and excellent in Asia)

Group 3

5	F	2,700,000 (66% tropical; most from Americas)

Group 4

6	UC	2,100,000 (40% tropical; CA, Mexico, Pacific)
7	CAS	2,000,000 (20% tropical; CA, Western North America, Madagascar)
8	DAO*	1,850,000 (Mainly North America especially Quebec)
9	MICH	1,750,000 (30% tropical; Regional, Mexico, some SE Asia & Pacific)
10	PH*	1,675,000 (25% tropical; WW, North American, some Pacific)

Group 5

11	RSA	1,183,000 (50% tropical; CA, also Mexico)
12	WIS	1,078,000 (50% tropical; North America and tropical America)
13	CAN*	1,010,500 (North America and Europe) Toronto
14	BRIT	1,010,000 (10% tropical; most from USA; recently Pacific and Peru)
15	TEX	1,006,000 (50% tropical; most Texas and Mexico, also tropical Americas)

Group 6

16	BPI	950,000 (Fungi WW, most temperate)
17	MIN	880,000 (10% tropical; Regional and Pacific)
18	BH	845,000 (10% tropical; Cultivated/economic, some China and Old World)
19	RM	806,800 (Temperate; Inter-mountain flora region)
20	DUKE	800,000 (35% tropical; Regional, West Indies, MesoAmerica)

Group 7

21	QFA	770,000 (North America)
22	BISH	750,000 (100% tropical, Pacific)
23	MT	745,000 (Regional, Canada)
24	NCU	665,000 (Regional, Carolinas)
25	BRY	661,100 (Regional, Utah)
26	UBC	660,000 (Regional, some Pacific)
27	MU	650,000 (35% tropical; North America, some South America and Pacific)

28	WTU	650,000 (Regional, W-USA, North Pacific rim)
29	ISC	640,000 (Regional, North America)
30	NA	600,000 (25% tropical; WW cultivated/economic, ethnobotanical)
31	ALTA	570,500 (10% tropical; Arctic and cordilleran Canada; Bryophytes of New World and Australia)
32	MSC	560,000 (20% tropical; WW especially North America, Mexico, Guatemala, Borneo, Patagonia)
33	TENN	(10% tropical mostly bryophytes; Regional, Mexico and Guatemala

second largest herbarium in the world (Group 1: 7,800,000) after P (8 million). Others in this top group include LE and K. The next North American herbarium (MO) is found in Group 2, along with G and L, and they each have ca. 6 million. Group 3, with ca. 5 million specimens, contains two North American herbaria (US, GH). So one third of the top 12 herbaria are found in North America, and they all house large collections from the tropics. This is followed by a large gap, and it is not until number 24 in Group 6 and number 28 in Group 7 that we find two more North American herbaria (F: 2,700,000 and UC: 2,100,000), both with large collections from North America and the tropics. These herbaria complete the list of the largest 34 herbaria in the world, only six of which are in North America.

Where on the list do we find herbaria that are actually located in the tropics? The two largest are BO (#30) and CAL (#31), both with 2 million specimens and both focused on regional diversity (Indonesia and India respectively). The largest herbarium in Asia is PE (#26, with a focus on China), and in Australia it is MEL (#51) and NSW (#52), both with 1,200,000, also with a regional focus. The sequential list in Table 2 includes all herbaria with 2,000,000 or more collections.

The excel file shows that in herbaria with an estimated size of 1–2 million specimens, there are two additional ones in North America (both in Canada with a north temperate focus), and three in Australia (with a national and/or regional focus; Table 2, Miscellaneous Group). There are five herbaria from tropical areas of the world in the Miscellaneous Group ranging from MEXU at 1,400,000 (focus on Mexico and Central America) to EA (East Africa) and IBSC (tropical and subtropical China) each with 1,000,000. Most of these tropical herbaria have a broad regional interest.

There are very few really large herbaria (Fig. 2): in North American size quickly falls to 1 million or less where it begins to taper off more gradually. There are six herbaria with 2 million or more specimens (less than 1% of the total number of herbaria in North American herbaria) and 16 with 1 million or more (2.4%). Globally, it drops to 2 million specimens before it begins to taper: there are 22 herbaria with 3 million or more (less than 1% of WW herbaria) and 34 with 2 million or more (1.26%).

The content of the collections in North American herbaria is based on past interests of the staff and/or administration or in some cases the interests of the Federal Government. Most herbaria in North America began by exploring local and regional plant diversity. However, there are exceptions, for instance, the US National Herbarium (US; Smithsonian Institution) was founded on the collections from the *United States Exploring Expedition* (under the command of Navy Lt. Charles Wilkes) which collected in western North America, South America and the Pacific in 1838–1842 and was charged with exploring the physical and biological diversity of the areas visited. It resulted in, among other items, 10,000 plant collections that became the foundation of the US National Herbarium. Over time, some herbaria became research centers with broader interests and greatly increased their holdings by diversifying into other areas of the world. In North America, nearly all of these large institutions were founded in the mid-1800's and have a large percentage of their collections from the Neotropics. Some have additional collections from the Pacific, Africa, Madagascar, and Asia. Most are weaker in Asia, Eurasia and Australasia, however there are exceptions such as GH (including AA) which has a long tradition of Asian exploration, MO with its collaboration with floras in Asia and Madagascar, and US with its history of work in the Pacific and the Philippines.

What is the Origin of the Collections in North American Herbaria?

Some herbaria have a good idea of the source of their collections. For instance, Field Museum estimates that 31% of their collections are from South American, 29% from Mexico and Central America, and 24% are from North American (M. Dillon pers. com.). Some herbaria have a partial record: US knows how many collections we have added starting in the early 1990's but prior to that it is more difficult. Other herbaria are using estimates that are closer to a guess. But most research staff have a sense of where their collections originated and are willing to share that information and those data are reflected in Table 3.

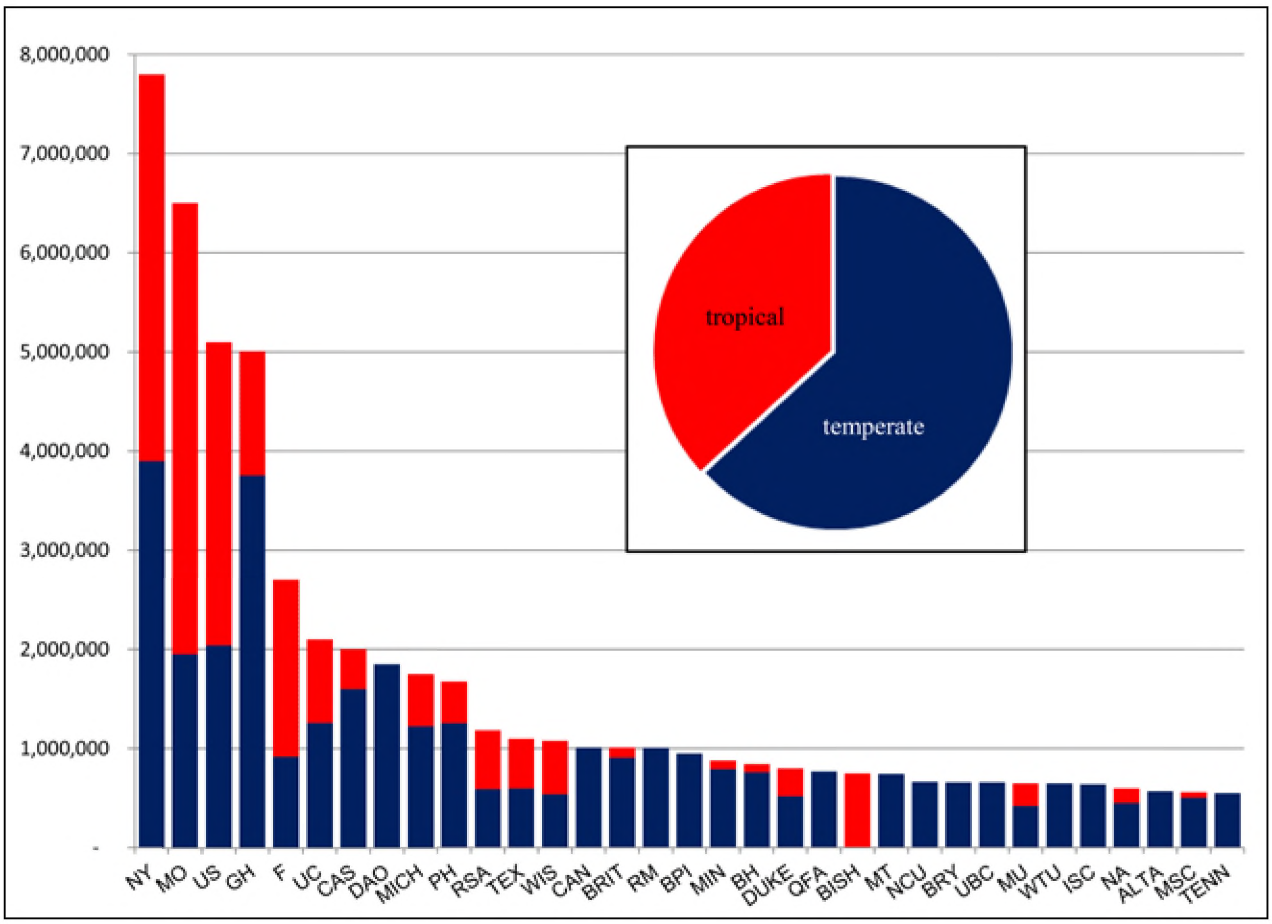


Fig. 3. Estimates of the number of specimens (Y axis) from the tropics in the 33 largest herbaria in North America. The pie-diagram shows the sum for these 33 herbaria.

There are 33 herbaria in North America with 550,000 or more specimens (Table 3). An examination of the list shows that beginning with MT (number 23) most of the collections are mainly regional with little tropical representation. There are exceptions, for instance MU (#27), NA (#30), and MSC (#32) have 20-35% of their collections from the tropics. And, even some of the larger herbaria do not have much in the way of tropical plants, for instance most Canadian herbaria have long focused on North American, mainly Canadian, plants in order to secure funding.

The vast majority of tropical specimens in North American herbaria are found in the largest herbaria. Table 3 and Figure 3 show that once herbaria have fewer than 1 million specimens they often have only a small percentage of specimens, if any, that are tropical, unless, of course, they are located in a tropical environment (e.g. BISH).

Approximately 20 million specimens from the tropics are in North American herbaria. This represents about 37% of the collections in the 30 largest herbaria and about 50% of the specimens in those with significant tropical holdings. These data show that the biggest impact on tropical research can be made by focusing on improving access to the 17 herbaria (out of 33) that have substantial holdings of tropical plants (Table 3).

How do we Evaluate the Importance/health of an Herbarium? Or indeed of the disciplines of plant taxonomy or systematics?

In looking at tropical plants housed in temperate herbaria, it is tempting to try and evaluate the health of herbaria that hold these important collections. How secure are these collections? Possible measures of success could be longevity, rate of increase in collection size, activity of faculty, staff, and students, or even number of grants and publications.

Table 4. Age of herbaria: North American herbaria founded before 1899 that are among the 33 largest herbaria in North America (Table 2). They are ranked by the date they were founded. **Red bold** indicates herbaria that are part of a university. Herbaria that were combined are indicated with an *.

Code (in 'Index Herbariorum'	Date of founding
PH	1812
MICH	**1837**
GH	**1842**
US	1848
WIS	**1849**
CAS	1853
MO	1859
MSC	**1863**
BPI	1869
ISC	**1870**
RSA	1872
UC	**1872**
CAN*	1882
WTU	**1882**
DAO*	1886
TENN	**1888**
MIN	**1890**
NY	1891
F	1893
RM	**1894**

Longevity

In North America 18 herbaria were founded before 1899 and are part of the list of North American Herbaria with more than 550,000 specimens (Table 3, 4).

Table 5. Age of herbaria in North America founded before 1850 with date of their founding and the current size of the collection. **Red bold** indicates the herbarium is one of the 30 largest in North America.

Code (in Index Herbariorum	Date	Number of specimens
SC	1771	1,500
CHARL	1773	25,000
MID	1800	2,500
PH	**1812**	**1,675,000**
PHIL	1821	13,000
DWC	1826	20,000
NYS	1836	278,662
MICH	**1837**	**1,700,000**
TRT	1838	370,000
UNB	1839	60,000
UCS	1840	8,000
GH	**1842**	**5,005,000**
US	**1848**	**5,100,000**

PH is the oldest (1812) and remains an important herbarium. The largest herbarium in North America, and the second largest in the world (NY) had a relatively late starting date (1891) but it has continued to prosper. It is interesting to note that Asa Gray, who was important in the founding of GH, was also important in the founding of MICH where he was located prior to moving to Harvard University. These two herbaria were founded five years apart. Three of the oldest large herbaria (MICH, GH, WIS) are university herbaria followed by those with a slightly later starting dates (ISC, UC, WTU, MIN, RM). So eight of the oldest large herbaria in North America are found at universities, a concept that is under siege in many places. Given the declining support for university herbaria one has to wonder if the administrators of herbaria at colleges and universities are aware of the importance of these herbaria, not only in housing irreplaceable collections but also in the training of undergraduates and preparing the next generation of systematists and biodiversity specialists, something museums often have difficulty in doing.

Thirteen herbaria in North America – that are still in existence – were founded before 1850 (Table 5). It is interesting to note that the age of an herbarium seems to have no correlation with its overall growth and current activity. For instance, in Table 5, the Herbarium codes in bold indicate presence of that herbarium in the list of largest 33 herbaria in North America: there are only four. Two of the earliest ones are both from South Carolina (USA) and remain small. In fact, although South Carolina has 12 herbaria in IH all but two are small and only two university collections, CLEMS (100,000 specimens) and USCH (122,000), have substantial holdings.

The age of North American herbaria pales in comparison to those in Europe. KASSEL, the oldest herbarium in the world – that is still in existence – was founded in 1569 (Table 6). The oldest one in North America (SC) is 22nd globally and the four largest herbaria in North America are far down the list with NY, the largest herbarium in North America and the second largest in the world, ranking 368. PH, the oldest large herbarium found in North America (Table 2), is 60th. However, like the herbaria in North America, the age of an herbarium globally is no predictor of continued growth as only six of the largest herbaria (Table 2) are found on the list of oldest herbaria (Table 6).

Number of herbaria founded

The largest growth in herbarium science in North America took place over a 50-year period from 1925 to 1974 (Fig. 4). Between those years, 365 herbaria were established all over North America. That is an average of 7–8 per year for 50 years. The largest gain was from 1950 to 1974 with 244 founded in 25 years, a rate of nearly ten per year. This increase is no doubt the result of the large amounts of government funding

Table 6. List of oldest herbaria world wide. **Red bold** indicates the herbarium is one of the 34 largest herbaria in the world (Table 2). **Blue bold** indicates North American herbaria. Herbaria that were combined are indicated with an *.

Rank	Code (in *Index Herbariorum*	Date	Number of specimens	Country
1	KASSEL	1569	30,000	Germany
2	BOLO	1570	130,000	Italy
3	BAS	1588	220,000	Switzerland
4	OXF	1621	500,000	UK
5	**P***	**1635**	**8,000,000**	**France**
6	ARG	1675	10,000	Malta
7	AMD	1700	at L	Netherlands
8	PARMA	1722	20,000	Italy
9	LINN	1730	33,800	UK
10	**S**	**1739**	**4,570,000**	**Sweden**
11	TO	1750	1,000,000	Italy
12	**H**	**1751**	**3,290,501**	**Finland**
13	**BM**	**1753**	**5,200,000**	**UK**
14	MA	1755	1,400,000	Spain
15	**C**	**1759**	**2,707,000**	**Denmark**
16	TRH	1760	430,000	Norway
17	KRMS	1761	28,000	Austria
18	CGE	1761	1,000,000	UK
19	MW	1765	989,240	Russia
20	LR	1770	77,000	France
21	LD	1770	2,500,000	Sweden
22	**SC**	**1771**	**1,500**	**USA**

End of consecutive numbers
Four largest North American Herbaria and PH (the oldest large herbarium).

60	PH	1812	USA
131	GH	1842	USA
139	US	1848	USA
177	MO	1859	USA
368	NY	1891	USA

(both state and federal) that were directed toward education and science during those years. But the following 25-year period (1975-1999) saw an unprecedented decline with a drop to a rate lower than the one for 1875-1899 and the most recent 15-year period produced only nine new herbaria. It is difficult to determine what caused this drop. It could be that the 'market' for herbaria in North America was saturated

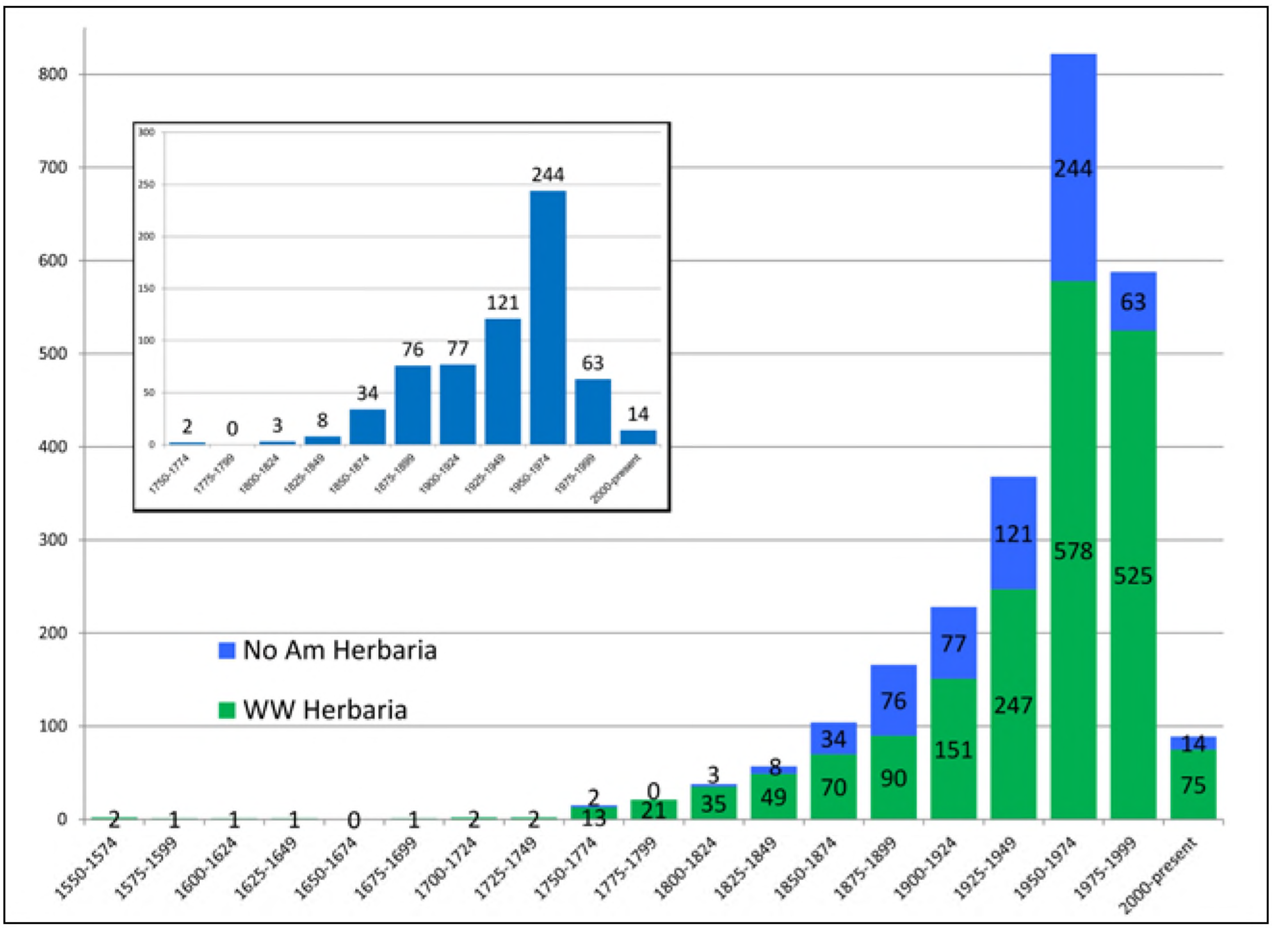


Fig. 4. The number of new herbaria (Y axis) founded in North America ('No Am Herbaria') in 25-year increments and the number of herbaria established world wide ('WW Herbaria').

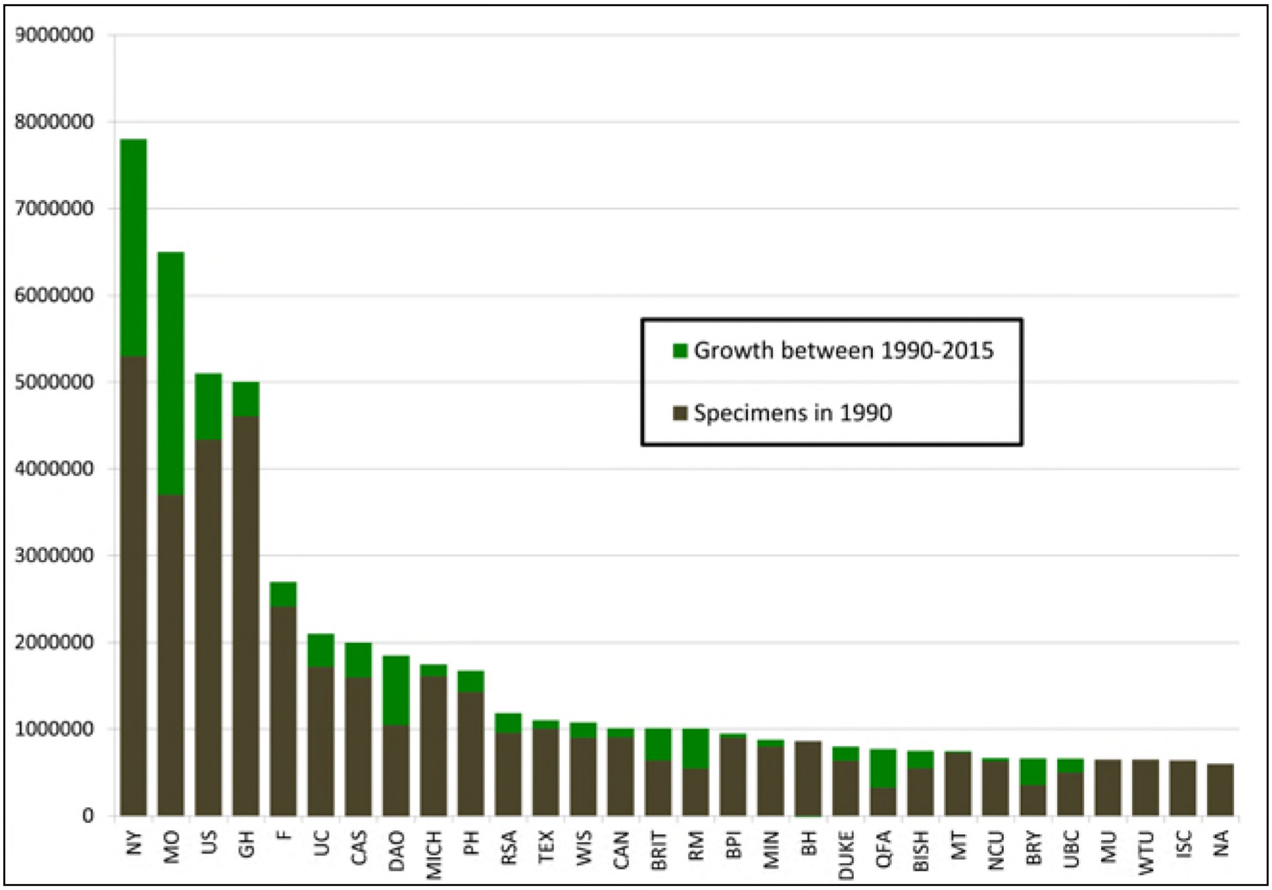


Fig. 5. Size of herbaria (measured by number of specimens – Y axis) in North American in 1990 and their growth between 1990 and 2015.

but it could also be a delayed response to more methods-driven research such as the modern synthesis (Huxley 1942) followed by phylogenetics (Hennig 1966) and the surge of molecular methods in the1990's.

How does this compare with the global rate of founding of new herbaria? The pattern is much the same, but the surge lasted longer (Fig. 4). The biggest increase took place 1950–1974 (nearly 33 per year), but non-North American herbaria continued to increase at nearly the same level for another 25 years while North American herbaria dropped off considerably (see above). This sustained growth seems to reflect new herbaria in the tropics, in fact, a rough count shows that the gains in the tropics were impressive: Tropical Americas 189, Asia-Pacific 170 (includes all of China), and Africa 48. So, a total of 407 of the total 588 new herbaria were in the tropics, corresponding to about 70%. But this too declined as we moved into the new century. The tropical countries with the largest gains were China (110 new herbaria), Brazil (47), Mexico (41), India (20), South Africa (17), and Argentina (14).

Increase in collection size through time

Perhaps the best way to judge how successful herbaria are is by looking at their productivity: how many collections are added, how many publications and grants, and how many students are trained. Most of these are elusive, but we can use the last published version of IH (Holmgren *et al.*, 1990) to evaluate growth in the collections.

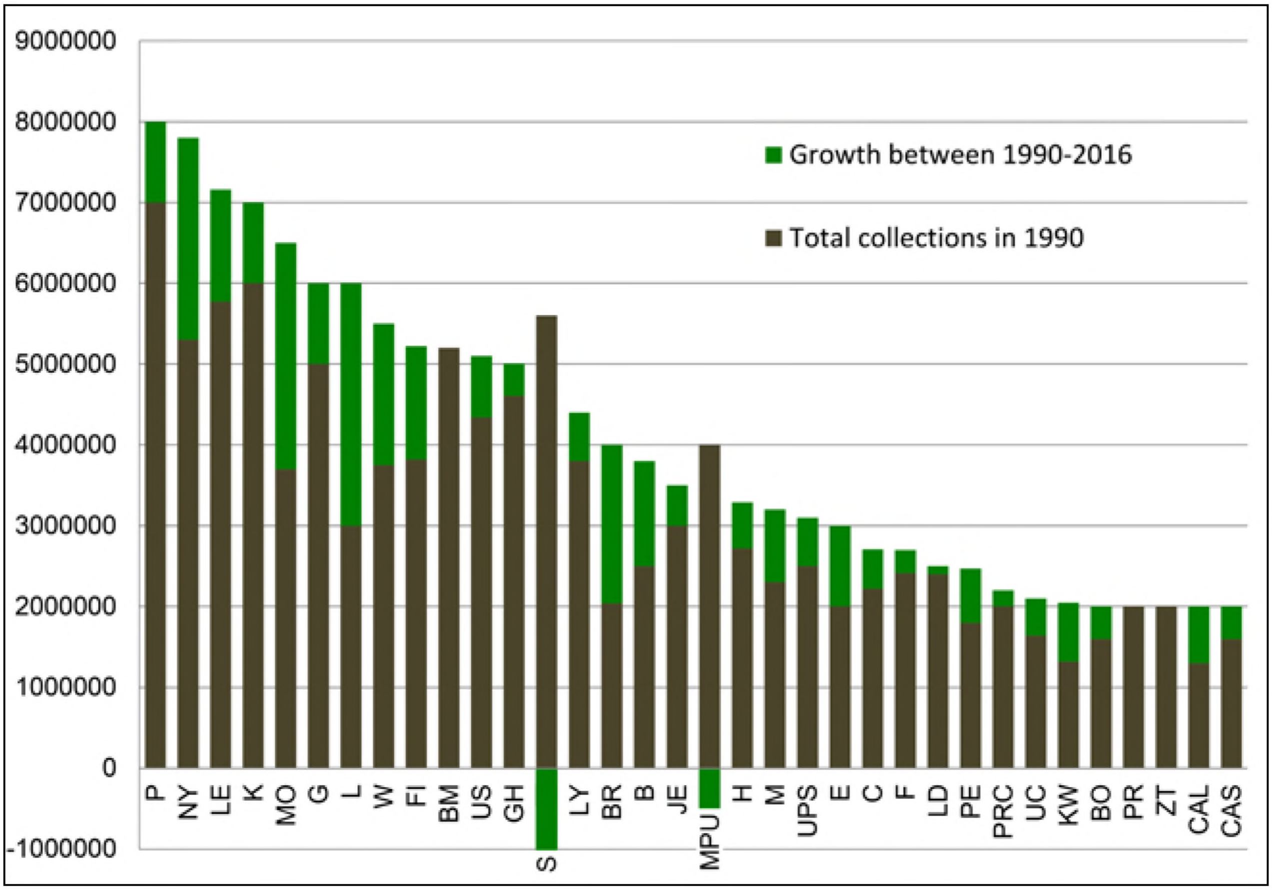


Fig. 6. Size of 34 largest herbaria world wide in 1990 (indicated by number of specimens – Y axis) and their growth in the number of herbarium specimens between 1990 and 2015. Note that several herbaria show no growth (BM, PR, ZT) and others show a negative growth (S, MPU); this is mostly caused by the current, more accurate, count of the existing specimens.

The last hard copy of *Index Herbariorum* was published in 1990 (Holmgren *et al.*) and information was taken from this publication to compare the size of institutions in 1990 versus their size now. The two largest institutions (NY and MO) generally increase their holdings by 80,000 to 100,000 per year (Fig. 5). They are in a league by themselves in regard to collections growth. Some of the growth comes from rescuing orphaned collections, but both herbaria have strong collecting and exchange programmes. US continues to add about 30,000 specimens per year mostly by processing the backlog and gift collections and a few collecting programs. Most other herbaria in North America add substantially less. One reason is the cost of staff to do the collecting and processing, because, to be useful, specimens must be collected, labeled, identified, mounted, and filed. As funding decreases or shifts to other priorities some major herbaria now add fewer specimens than smaller ones. This can be compared with the global herbarium community (Fig. 6) where MO and NY still stand out as having the largest average yearly increase but several others have added a million or more specimens in the last 25 years, including BR, FI, G, K, LE, P, and W. How much of this increase is the result of expeditions and how much comes in as exchange or gifts (e.g., for determination) or even the incorporation of other once independent herbaria (e.g., L), is yet to be determined. Some institutions show a decrease in size or zero increase which is often caused by doing an exact count of all the collections.

In order to discuss growth we need to examine the question: What drives growth? After talking to fellow museum and garden scientists about this question it seems that there are a number of factors:

1. Focus of the director of the institution (e.g. K, NY)
2. Participation in floras and surveys (e.g. K, L, MO, P, US)
3. Availability of funding (e.g. NSF)
4. Availability of jobs for students during degree process and upon graduation
5. Acknowledged importance of expeditions and systematics by scientific community and the government

As an example of the importance of leadership, we can cite the first two directors of K (William Jackson Hooker and Joseph Dalton Hooker) who set the stage for the institution we see today. They were scholars, explorers, and tireless promoters of their institution. Joseph Dalton Hooker took part in several years-long expeditions. On one, the Antarctic voyage of the Erebus and Terror under the command of Captain Sir James Clark Ross (1839-1843), Hooker studied the flora of the circumpolar Antarctic region and developed hypotheses that influenced the discipline of biogeography. They were not just administrators, they were visionary leaders in the scientific community and the development of their institution reflected their dedication and knowledge (Allan 1967). An example from North America is Peter Raven, who became director of MO in 1971 and retired in 2011. During his tenure, he transformed a good mid-western herbarium into a powerhouse of specimen based plant science. Currently, systematists do not run most major herbaria although there are exceptions (e.g. M, MO, RSA). All of the large herbaria organized floras and surveys for tropical areas such as the Amazon (NY), Asia (GH, L), Madagascar (P, MO), MesoAmerica (BM, MO), and the Pacific (P, US).

Equally important in successful herbaria is the ability to generate funding to help offset the cost of expeditions and infrastructure. In the USA, the National Science Foundation (NSF) has had several programs to accomplish this, but sadly, this has all but stopped, and recently it even canceled the call for biological infrastructure proposals. Many other countries are also cutting back on their funding for collections and expeditions that supply new material, leaving institutions with less funding and hence slower growth. Infrastructure includes the training of students and postdocs, but this is limited by the availability of jobs when they graduate. Perhaps the biggest problem is the lack of recognition of the importance of collections in shaping our view of the world.

Relationships between Temperate and Tropical Herbaria

The development of larger North American herbaria (those that hold most tropical collections) seems to follow a common trajectory (with exceptions to all steps):

Step 1: The herbarium founder(s) have a goal of establishing an herbarium to document local and regional diversity.

Step 2: The director and staff become interested in how their flora compares to plants from other parts of the world, and they begin to expand their geographic sphere of interest to gain a better idea of global plant diversity. Most specimens are brought back to the country of the collector. In the case of collections supported by federal governments a herbarium may be asked to take specimens from government-backed expeditions (e.g. the US Exploring expedition funded by the US government helped found the National Museum of Natural History).

Step 3: The development of a local scientific community results in scientists in the tropics asking questions about why all of the biodiversity samples are being removed from the country. Without adequate libraries and access to historical collections, they are hard pressed to study their own biodiversity. Naturally, this creates a tension between the scientists in tropical countries and the large temperate herbaria.

Step 4: Exchange of information starts, students are trained, resources are shared, field trips are joint ventures, etc. which is certainly a great progress. But nearly all of the historical materials remain in temperate herbaria (e.g. publications and type specimens).

Step 5: Global and local efforts are initiated to share the information (in both directions). These began gradually, but in recent years, with the advent of big data and global programs, they have transformed the way we work.

Botanists have always worked as a group, and as a result they consistently have been better organized than other fields of research. Many of these still-active projects were begun under the auspices of the International Association for Plant Taxonomy (IAPT), then housed in Utrecht (U); sadly this herbarium no longer exists as an independent unit having been integrated into L. But, because of their foresight we have many resources that are useful to botanists around the world. Index herbariorum: Part I. The Herbaria of the World (Theirs continuously updated), was started in 1952; the International Plant Names Index (IPNI, http://www.ipni. Org; Croft *et al.* 1999), is a collaboration among the Royal Botanic Gardens, Kew (the Index Kewensis was first published in 1885), the Harvard University Herbaria (The Gray Cards Index), and the Australian National Herbarium (Croft *et al.* 1999; Lughadha 2004); *Index Herbariorum II Collectors* (Lanjouw & Stafleu) was first published in 1954; *Taxonomic Literature*, a compendium of taxonomic publications, was first published in 1967 (Stafleu) and is now an amazing online resource (http://www.sil.si.edu/digitalcollections/tl-2/).

More recent efforts have build on this foundation of sharing knowledge and the community now has TROPICOS, developed by MO over the past 30 years, that gives us lists of specimens and localities as well images and references and more (http://www.tropicos.org/Home.aspx). Later the Global Biodiversity Information Facility (GBIF) was established (1999; http://www.gbif.org/). It provides locality information for all of life. This was (and is) an amazing concept and one that most scientists can support. Although the data in GBIF are not curated in a consistent manner (see Goodwin *et al.* 2015), it is a useful tool and one that the community should work to improve (see the recent survey published on line as http://www.gbif.org/newsroom/news/fitness-for-use-report-distribution-modelling). Other efforts to share information are the Biodiversity Heritage Library (BHL) that makes older literature available (http://www.biodiversitylibrary.org/bibliography/48631-/summary) and JSTOR Global Plants, which hosts images of type specimens (http://about.jstor.org/content/global-plants).

In addition, museums, gardens, and universities around the world strive to make the collections they house and their associated data available to the global community. There are many examples of these efforts such as the well-known *Australia's Virtual Herbarium* (Council of Heads of Australasian Herbaria 2013; http://avh.chah.org.au/). Some countries are working hard to make their herbarium collections available globally including France, the Netherlands, the United States, and China, where progress has been made in digitizing herbarium collections and in disseminating the information. In fact, the world's largest herbarium (P) was mostly digitized during its recent physical renovation (https://science.mnhn.fr/). Concerning North America, the US Virtual Herbarium project (USVH, http://usvhproject.org/; Barkworth & Murrell, 2012) is underway, and, if successful, it will make available most of the large tropical collections in North America (Beaman & Cellinese 2012), although federal collections are excluded.

Finally, the way we disseminate our data has changed. The years-long wait for publications to be freely available has given way to rapid publication and 'open access'. A few new journals have been designed to rapidly publish the taxonomic work. Pioneered by Pensoft (http://www.pensoft.net/; e.g. *Phytokeys*), a leading publisher of open access cybertaxonomy, this effort really became practical after changes made in the International Code of Nomenclature for algae, fungi and plants (McNeill *et al.* 2012) began to allow electronic publication and the use of English in descriptions of new taxa (Miller *et al.* 2011). These journals disseminate biodiversity data in both traditional and innovative ways, and register all new nomenclature with databases such as the International Plant Names Index (IPNI) (http://www.ipni.org/).

The result of all of these innovations (and more that are not mentioned here) is the empowerment of our colleagues from tropical countries. They now have the ability to view the types and much of the literature that they need. Their herbaria have grown to the extent that they have much better access to recent material, and they are able to interact globally. The future will bring many additional online resources (i.e. more specimens and literature) as these data sharing efforts continue. As a result much of the tension has dissipated, and botanists from temperate and tropical areas are working together and separately to achieve our common goal of understanding the botanical diversity of Earth. One definition of a friend is "someone who accepts your past, supports your present, and encourages your future" and I think temperate and tropical botanists are now, and really have been for some time, friends.

Afterward

This paper is an outgrowth of my longstanding interest in the health and utility of biodiversity collections (especially herbaria) and their ancillary collections (Funk 2003a, 2003b, 2006, 2014). Mine is not the only voice on this topic, and the literature is littered with the efforts of many (see citations in the Introduction and use Google Scholar to find many additional ones) to stem the receding tide of funding that sucks away our ability to mount expeditions, conduct research, maintain collections, and train the next generation of systematists. This is especially true in most temperate areas, but also in Australia and the Pacific. Although there are some successes, largely these efforts have failed, and the number of herbaria that drastically reduce their staff and store or give away their collections grows at an ever-increasing pace. Despite the overall lack of success, we must not quit because it is possible that eventually, if it is said often enough, the importance of biological collections and the research that results from them will be recognized for its relevance to understanding and preserving life on our planet. It is now time for the herbaria of the topical and temperate areas of the world to work together using our newfound unity to demonstrate the power of herbaria to administrators and funding agencies (Conniff, 2016).

For surely "We must all hang together, or we shall surely all hang separately." (Benjamin Franklin, at the signing of the Declaration of Independence).

Acknowledgements

I thank Professors Ib Friis (C) and Henrik Balslev (AAU) for the invitation to speak at the symposium and prepare this paper and Barbara Thiers (NY) and Jim Solomon (MO) for conversations and Thiers for the use of the data from *Index Herbariorum*. I especially appreciate the updates the new information from staff at some of the herbaria who helped me update *Index Herbariorum*: Arne Anderberg (S); Dave Bufford (GH); Mike Dillon (F); Ron Hartman (RM); Lucinda McDade (RSA); Alan Prather (MSC); Kathleen Pryor (DUKE); Jim Solomon (MO); B. Eugene Wofford (TENN); and Beryl Simpson (TEX). Carol Kelloff (US) kindly checked all the totals in the tables and figures.

References

Allan, M. (1967). *The Hookers of Kew.* Michael Joseph, London.

Beck, J.B. & Semple, J.C. (2015). Next-generation sampling: Pairing genomics with herbarium specimens provides species-level signal in *Solidago* (Asteraceae). *Applications in Plant Sciences* 3(6): 1500014.

Conniff, R. (2016). Our natural history – endangered. *The New York Times on line*: http://www.nytimes.com/2016/04/03/opinion/ournatural-history-endangered.html?ref=collection%2Fcolumn%2Frichard-conniff&action=click&contentCollection=opinion&region=stream&module=stream_unit&version=latest&contentPlacement=1

&pgtype=collection [A version of this op-ed appeared in print on 3 April 2016, on page SR4 of the New York edition with the headline: Natural History, Endangered.]

Croft, J., Cross, N., Hinchcliffe, S., Lughadha, E.N., Stevens, P.F., West, J.G. & Whitbread, G. (1999). Plant names for the 21st century: The International Plant Names Index, a distributed data source of general accessibility. *Taxon* 48: 317–324.

Barkworth, M.E. & Murrell, Z.E. (2012). The US Virtual Herbarium: Working with individual herbaria to build a national resource. *ZooKeys* 209: 55–73.

Beaman, R.S. & Cellinese, N. (2012). Mass digitization of scientific collections: New opportunities to transform the use of biological specimens and underwrite biodiversity science. *ZooKeys* 209: 7–17.

Council of Heads of Australasian Herbaria. (2013). *Australia's Virtual Herbarium*. Available at http://avh.chah.org.au/

Ellis, E.C., Antill, E.C. & Kreft, H. (2012). All is not loss: Plant biodiversity in the Anthropocene. *PLoS ONE* 7(1): e30535. doi:10.1371/journal. pone.0030535.

Fant, J.B., Havens, K., Keller, J.M., Radosavljevic, A. & Yates, E.D. (2014). The influence of contemporary and historic landscape features on the genetic structure of the sand dune endemic, *Cirsium pitcheri* (Asteraceae). *Heredity* 112: 519–530.

Feeley, K.J. (2012). Distributional migrations, expansions, and contractions of tropical plant species as revealed in dated herbarium records. *Global Change Biology* 18: 1335–1341.

Funk, V.A. 2003a. The importance of herbaria. *Plant Science Bulletin* 49: 94–95.

Funk, V.A. (2003b). 100 uses for an herbarium (well at least 72). *ASPT Newsletter* 17: 17–19.

Funk, V.A. (2006). Floras: A model for biodiversity studies or a thing of the past? *Taxon* 55: 581–588.

Funk, V.A. (2014). The erosion of collections-based science: Alarming trend or coincidence? *The Plant Press*, new series 17(4): 1, 14–15. [Editorial]

Goodwin, Z.A., Harris, D.J., Filer, D., Wood, J.R.I. & Scotland, R.W. (2015). Widespread mistaken identity in tropical plant collections. *Current Biology* 25(22): R1066–R1067

Holmes, M.W., Hammond, T.T., Wogan, G.O.U., Walsh, R.E., Labarbera, K., Wommack, E.A., Mattins, F.M., Crawford, J.C., Mack, K.L., Bloch, L.M. & Nachman, M.W. (2016). Natural history collections as windows on evolutionary processes. *Molecular Ecology* 25: 864–881.

Holmgren, P.K., Holmgren, N.H. & Barnett, L.C. (1990). *Index Herbariorum. Part I: The Herbaria of the World*. IAPT by New York Botanical Garden, Bronx, New York.

Huxley J. (1942). *Evolution, the Modern Synthesis*. Harper & Brothers, New York.

Johnson K.G., Brooks S.J., Fenberg, P.B., Glover, A.G., James K.E., Lister, A.M., Michel, E., Spencer, M., Todd, J.A., Valsami-Jones, E., Young, J.R. & Stewart, J.R. (2011). Climate change and biosphere response: Unlocking the collections vault. *BioScience* 61: 147–153.

Kemp, C. (2015). The endangered dead. *Nature* 518: 292–294.

Lanjouw, J. & Stafleu, F.A. (1954). *Index Herbariorum Part II: Collectors*. International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy, Utrecht.

Lughadha, E. (2004). Towards a working list of all known plant species. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359: 681–687.

Manos, P.S. & Meireles, J.E. (2015). Biogeographic analysis of the woody plants of the southern Appalachianas: Implications for the origins of a regional flora. *American Journal of Botany* 102: 780–804.

Martin, M.D., Zimmer, E.A., Olsen, M.T., Foote, A.D., Gilbert, M.T.P. & Brush, G.S. (2014). Herbarium specimens reveal a historical shift in phylogeographic structure of common ragweed during native range disturbance. *Molecular Ecology* 23: 1701–1716 doi: 10.1111/mec.12675

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012). International code of nomenclature for algae, fungi, and plants (Melbourne code) adopted by the 18th International Botanical Congress, Melbourne, Australia, July 2011. *Regnum Vegetabile* 154.

Miller, J.S., Funk, V.A., Wagner, W.L., Barrie, F., Hoch, P.C. & Herendeen, P. (2011). Outcomes of the 2011 Botanical Nomenclature Section at the XVIII International Botanical Congress. *PhytoKeys* 5: 1–3.

Primack, D., Imbres, C., Primack, R.B., Miller-Rushing, A.J. & Del Tredici, P. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91: 1260–1264.

SA2000 [Systematics Agenda 2000]. (1994). *Charting the Biosphere: A Global Initiative to Discover, Describe and Classify the World's Species*. Technical report. New York: American

Society of Plant Taxonomists, Society of Systematic Biologists, and the Willi Hennig Society, 34 pages.

Schilthuizen, M., Vairappan, C.S., Slade, E.M., Mann, D.J. & Miller, J.A. (2015). Specimens as primary data: Museums and 'open science'. *Trends in Ecology and Evolution* 30: 237–238.

Stafleu, F.A. (1967). *Taxonomic Literature*. International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy, Utrecht.

Thiers, B [continuously updated]. *Index Herbariorum: A global directory of public herbaria and associated staff.* New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/

Wen, J., Ickert-Bond, S.M., Appelhans, M.S., Dorr, L.J. & Funk, V.A. (2015). Collections-based systematics: Opportunities and outlook for 2050. *Journal of Systematics and Evolution* 53: 477–488

Appendix. Location of the ca. 100 herbaria mentioned in this paper (alphabetical by code) and an indication of the ones that were combined for calculations in this study. For more information see *Index Herbariorum* (Thiers (continuously updated)). Herbaria that were combined are indicated with an *.

Abbreviation	City	Country
AD	Adelaide	Australia
ARG	Floriana	Malta
ALTA	Edmonton, Alberta	Canada
AMD (housed at L)	Leiden	Netherlands
B	Berlin	Germany
BAS		Switzerland
BH	Ithaca NY	USA
BISH	Honolulu HI	USA
BM	London	UK
BO	Bogor	Indonesia
BOLO	Bologna	Italy
BP	Budapest	Hungary
BPI	Beltsville MD	USA
BR	Meise	Belgium
BRIT	Ft Worth TX	USA
BRY	Provo UT	USA
C	Copenhagen	Denmark
CAL	Howrah, Kolkata	India
CAN+CANA+-CANL+CANM*	Ottawa QC	Canada
CANB	Canberra	Australia
CAS	San Francisco	USA
CGE	Cambridge	UK
CHARL	Charleston SC	USA

Abbreviation	City	Country
CLEMS	Clemson SC	USA
DAO+DAOM*	Ottawa QC	Canada
DUKE	Durham NC	USA
DWC	West Chester PA	USA
E	Edinburgh	UK
EA	Nairobi	Kenya
ENCB	Mexico City	Mexico
F	Chicago IL	USA
FI	Florence	Italy
G	Geneva	Switzerland
GH	Cambridge	USA
H	Helsinki	Finland
HBG	Hamburg	Germany
IBSC	Guangzhou	China
ISC	Ames IA	USA
JE	Jena	Germany
K	Kew	UK
KASSEL	Kassel	Germany
KRMS	Kremsmunster	Austria
KUN	Kunming	China
KW	Kiev	Ukraine
L	Leiden	Netherlands
LD	Lund	Sweden
LE	Leningrad (St Petersburg)	Russia
LINN	London	UK

Abbreviation	City	Country
LR	La Rochelle	France
LY	Lyon	France
M	Munich	Germany
MA	Madrid	Spain
MEL	Melbourne	Australia
MEXU	Mexico City	Mexico
MICH	Ann Arbor MI	USA
MID	Middlebury VT	USA
MIN	Saint Paul MN	USA
MO	Saint Louis MO	USA
MPU	Montpellier	France
MSC	East Lansing MI	USA
MT	Montreal QC	Canada
MU	Oxford OH	USA
MW	Moscow	Russia
NA	Washington DC	USA
NCU	Chapel Hill NC	USA
NSW	Sydney	Australia
NY	New York NY	USA
NYS	Albany NY	USA
O	Oslo	Norway
OXF	Oxford	UK
P+PC*	Paris	France
PARMA	Parma	Italy
PE	Beijing	China
PH+ANSP*	Philadelphia PA	USA
PHIL	Philadelphia PA	USA

Abbreviation	City	Country
PR	Prague	Czech Republic
PRC	Prague	Czech Republic
PRE	Pretoria	South Africa
QFA	Quebec QC	Canada
RM	Laramie WY	USA
RSA	Claremont CA	USA
S	Stockholm	Sweden
SC	Winston-Salem SC	USA
TENN	Knoxville TN	USA
TEX	Austin TX	USA
TI	Tokyo	Japan
TNS	Tsukuba	Japan
TO	Torino	Italy
TRH	Trondheim	Norway
TRT	Toronto ON	Canada
UBC	Vancouver BC	Canada
UC	Berkeley CA	USA
UCS	Schenectady NY	USA
UNB	Fredericton NB	Canada
UPS	Uppsala	Sweden
US	Washington DC	USA
USCH	Columbia SC	USA
W	Vienna	Austria
WIS	Madison WI	USA
WTU	Seattle WA	USA
ZT	Zurich	Switzerland